THE RAT'S REACTION TO A PREDATOR:

MODIFICATION BY CHLORDIAZEPOXIDE

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CONTENTS

ABSTRACT

The modification of species-specific defense reactions in rats by chlordiazepoxide was investigated in a multifactorial design (2 x 2 x 2 x 2) using strain, sex, predator and drug as independent variables. A number of dependent variables measured freezing and escape, and the results were analysed by a multivariate analysis of variance programme.

Presence of a predator was found to significantly increase freezing, immobility and locomotion. Latency to leave close proximity to the stimulus animal was not significantly changed by presence of the predator but escape was facilitated. Availability of an extra area to escape into was not important, since animals escaped from close proximity to the predator but not as far away as possible. Wistar rats were more reactive to the predator than Hoodeds.

Administration of chlordiazepoxide significantly increased immobility (and there was a nonsignificant trend for this increase to be higher in the predator condition) and increased time in close proximity to the stimulus animal, while reducing time in the far end of the runway. There was no firm evidence for weakening of escape behaviour by chlordiazepoxide.

Grooming and sniffing were not very useful variables but rearing was decreased in the presence of a predator. Approach-avoidance conflict was observed in the presence of the predator and this was decreased by chlordiazepoxide.

It was concluded that while many earlier observations were upheld, the present design had yielded much useful information especially on drug administration. Conclusions

about the role of brain structures responsible for eliciting and maintaining species-specific defense reactions were considered to be premature.

The notion of species-specific defense reactions was productive although some modification and extension of the dependent variables previously used to measure defensive reactions is indicated.

Keywords: species-specific defense reactions - predator - chlordiazepoxide - freezing - escape - rats.

CHAPTER 1

INTRODUCTION

1.1 GENERAL AREA: SPECIES-SPECIFIC DEFENSE REACTIONS AND AVOIDANCE

Increasingly over the last decade there have been challenges to some of the basic laws of learning, particularly in relation to avoidance learning.

Some authors, especially Seligman (1970), have suggested that there are no general laws of learning and that any laws based on arbitrary events are not general, but peculiar to such events. Seligman stated that a basic premise which he called the assumption of equivalence of associability, lies at the heart of general process learning theory. This assumption is that the particular stimuli, responses and reinforcers chosen are arbitrary: any emitted response and any reinforcer can thus be associated with equal ease. Seligman challenged this assumption and suggested that organisms may be more or less prepared by the biological evolution of their species to associate a given conditioned stimulus and unconditioned stimulus; thus the laws of learning may vary with this preparedness. An operational definition of preparedness is:

> "the relative preparedness of an animal for learning about a contingency is defined by how degraded the input can be before the output reliably occurs which means that learning has taken place" (Seligman & Hager, 1972 p4).

Speed of acquisition of response demonstrates preparedness: unpreparedness is demonstrated if many pairings are required and contrapreparedness if the response is not learnt at all.

There are many examples in the literature which cite a failure to learn. Breland and Breland (1972) described how their animals' species-specific food-getting behaviour disrupted the behaviour that the Brelands were trying to train even though in many instances this disruption delayed reinforcement. This phenomenon they labelled 'instinctive drift'. Garcia and Koelling (1966) demonstrated preparedness in their experiments on the phenomena of taste-aversion learning. Wilcoxin, Bragoin and Kral (1971) also argued that selectivity of taste-illness association is an example of preparedness. Thorndike (1964) found difficulty in getting cats to groom to escape from a box and he suggested the animals may not have been neurally prepared to connect this behaviour with sense impressions. Lenneberg (1967) noted long elaborate training is not required for speech in humans and Gardner and Gardner (1970) explained failures to teach chimpanzees speech by the contraprepared nature of vocalization in this species. Bolles (1970), Rozin and Kalat (1971), Shettleworth (1972), Staddon and Simmelhag (1971) discuss the relation between experimental factors and organismic predispositions in greater detail.

In the avoidance area, it has been found difficult to train arbitrary responses (such as bar pressing) to be avoidance responses. In particular it is very difficult to train pigeons to key peck to avoid shock (Rachlin and Hineline, 1967) while other responses such as flying and wingflapping

have been easily trained (Rachlin, 1969). It is also difficult to train rats to bar press to avoid shock reliably (D'Amato and Fazzaro, 1966; Fantino, Sharp and Cole, 1966). The difficulties encountered suggest that the nature of the required operant may be interfering with learning. Some writers have suggested the difficulties encountered are due to the required response never having been established. However, Schwartz and Coulter (1973) trained pigeons to key peck for food reinforcement and failed to transfer this response to avoidance and escape from shock. Thus it seems unlikely that failure to learn is due to the response never having been established.

Seligman (1970) concluded

> "The premise of equivalence of associability does not hold <u>even in the traditional paradigms for which it was first assumed</u>" p415 (his italics).

The implications of such a conclusion are that there should be a re-examination of some of the basic premises of learning theory in the light of a preparedness continuum.

There have been some criticisms and replies to Seligman. Doyle (1971) suggested that personal as well as evolutionary history is involved and that encounters between the organism and his environment determine the direction of development of inherited structures. Schwartz (1974) said the preparedness concept is circular unless it means more than just ease of learning. In fact, he stated:

> "the concept of preparedness as presently defined does not facilitate a reformulation (of our most fundamental principles and categorizations) and may even serve to fortify our current one" (p188).

The circularity implicit in preparedness is its dependence upon the paradigms that the phenomena are being evaluated against. There are no clear definitions other than the procedures themselves for labelling the phenomena as certain types of learning. Furthermore, Schwartz pointed out the preparedness notion may obscure the distinction between ontogenetic and phylogenetic contributions. A very important point made by Schwartz is that the significance of preparedness may vary from species to species so that simpler organisms may profit less from experience than more complex organisms. Despite these criticisms, it is apparent that preparedness cannot be ignored. The weight of studies which have found difficulty in establishing learning in some instances, leave the assumption of equivalence of associability open to question.

A specific example of the preparedness dimension is Bolles' (1970a) notion of Species-Specific Defense Reactions (SSDRs). Early in the 1960s some of the problems facing learning theorists in the area of avoidance became focussed on what Bolles (1972b) calls the response problem or 'why are some avoidance responses so much more readily learned than others?" (p119). Avoidance has always been difficult to explain by the reinforcement theorist as no explicit event can be labelled as a reinforcer. Traditionally, three factors are cited as sources of reinforcement: (i) the escape contingency and (ii) the CS-Termination contingency. However Bolles (1969) said that for both of these contingencies what is important is what response is required of the subject. When the avoidance response is an SSDR, neither conditioned stimulus termination nor feedback stimulus presentation (FS) are

important. (Bolles, Moot and Grossen , 1971; Bolles, Stokes and Younger, 1966; D'Amato and Fazzaro, 1966).

(iii) The Avoidance contingency - however Bolles (1969) suggested the topography of an avoidance response is less important than its functional properties. Other theories have also been proposed to explain avoidance. For example, freezing competing with bar pressing (Meyer et al. 1960) a discrimination hypothesis (D'Amato, 1967) and inadequate-reinforcement (Brush, 1962; Masterton, 1970).

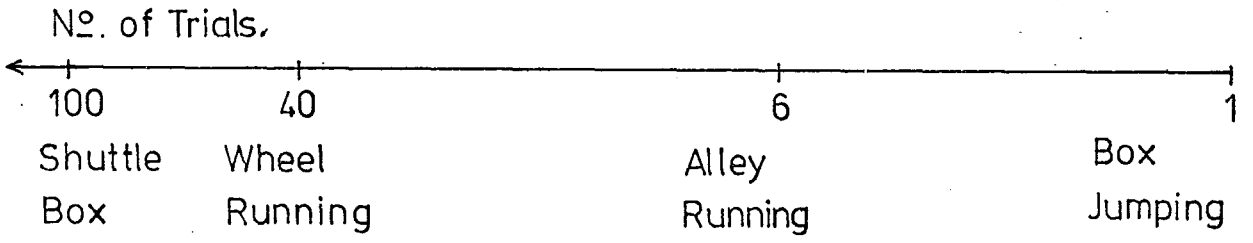
Bolles (1970a) in an expansion of Gibson's (1952) early observations, proposed a hypothesis which accounts for the failures to show avoidance learning in the laboratory. He argued that in the wild, in order to survive, animals use innate defensive reactions which vary from species to species and these occur whenever the animal encounters any new or sudden stimulus. These SSDRs generally have three forms: freezing, running away and aggression. Furthermore, Bolles argued these reactions are always near threshold so that they can occur rapidly.

> "Neither the mouse nor the gazelle can afford to learn to avoid; survival is too urgent, the opportunity to learn is too limited, and the parameters of the situation make the necessary learning impossible. The animal which survives is one which comes into its environment with defensive reactions already a prominent part of its repertoire" p33 (his italics).

Bolles suggested the laboratory or domestic animal is converted in the presence of noxious stimuli, at least temporarily, into a wild animal by restricting its response repertoire

into SSDRs. Failures to learn avoidance, suggest the response required was not an SSDR and rapid acquisition of the response would have only been possible if the response required was an SSDR. Bolles (1970a) argued that a continuum of difficulty of avoidance learning may exist, with SSDRs at one and arbitrary learning at the other. This could be represented by Figure 1.

A Continuum of Difficulty of Avoidance Learning



Some responses take hundreds of trials to learn and may in fact never be learnt at all (Brush, 1966) whilst others can be learnt in one trial (Maatsch, 1959).

Some SSDRs are competitive - one cannot run and freeze at the same time - and when competition occurs, which SSDR becomes dominant depends on the characteristics of the situation. If escape is possible, then escape will occur, but if the situation is inescapable those defense reactions relating to escape from the noxious stimuli will be suppressed and the remaining SSDR will emerge as dominant. In the (1970a) paper, Bolles stated an avoidance response can be learned only if it is an SSDR. In order to explain why some arbitrary responses are eventually learned, Bolles revised his theory in 1972. This stronger version argued that Feedback Stimulus and

Safety Signal (a concept developed by Rescorla and Lo Lordo (1965) which suggested Safety Signal inhibits fear) are functionally equivalent in that they predict safety. Bolles (1972b) suggested Danger Signals release SSDRs whilst Safety Signal release alters behaviours in the response repertoire so that Safety Signal acts as a de-motivator, suppressing avoidance behaviour. All behaviour then consists of SSDRs, the topography of which is determined in part by the animal's expectation of danger and safety, and in part by the structure of the environmental stimuli If the situation looks like a place to run, the animal runs and if the situation looks inescapable, it freezes. The importance of conditioned noxious stimuli is therefore that they predict shock rather than because they are paired with it. When the Danger Signal occurs, predicting noxious stimuli, SSDRs are released but if a response other than a SSDR is required, the SSDRs will be punished and a close variant of the SSDR will persist (Bolles 1975a). This in part explains why some animals learn to bar press. The animal may actually be freezing while holding onto the bar as this is the only response which is also an SSDR and enables survival (Bolles and McGillis, 1968; Bolles and Riley, 1973). Peterson and Lyon (1975) suggested freezing on the bar is a prerequisite for lever pressing. They found manipulation of lever pressing so it approximated an SSDR, facilitated acquisition of lever-press shock avoidance. The manner in which lever pressing is acquired (if at all) is that flight is perceived as impossible so the next most potent SSDR (freezing) occurs and specifically on the lever. Eventually the subject discriminates that the arbitrary response of bar pressing

also predicts safety. Bolles went further to say that whether an animal learns the required response depends on how removed it is from the SSDR repertoire and how much safety the response produces.

Support for the SSDR theory has come from a number of authors (Schwartz, 1974; (with revision) Seligman, 1972; and Smith, Gustavsen and Gregson, 1972). The latter authors concluded the difficulty in learning key-pecking by pigeons during shock was from interference from the unconditioned flexion response and this is compatible with SSDR theory.

The SSDR theory has been seen as circular in its argument: an avoidance response is learned rapidly only if it is an SSDR and if a response is learnt rapidly then it is an SSDR. Thus, the definition of an SSDR seems to be post hoc. Seligman and Hager (1972) suggested observation of a species' reactions to a natural predator in order to define SSDRs, may break through the circularity. Schwartz (1974) agreed the circularity would be broken by independent assessment of what behaviours are SSDRs in the wild. Bolles (1972) claimed there is no circularity as the definitions of SSDRs are easily seen by shocking rats and observing what occurs. However, naturalistic observations are important in an area such as this. Bolles rejected the notion that non-SSDRs will fail simply because they never occur. In fact Schwartz and Coulters' (1973) experiment ensured that they did occur and still failed to establish learning. The SSDR hypothesis is thus not just an argument about operant level.

Bolles has argued persuasively for the acceptance of SSDRs to explain the response problem of why some avoidance responses are more readily acquired than others and has led us to the point where further research is essential for clarification. Consideration of the general literature and specifically the notion of preparedness in the light of SSDR theory, suggests that circularity of the argument can be countered by consideration of ethological-type studies which observe animals' reactions to a naturally dangerous situation.

1.2 SPECIFIC PERTINENT RESEARCH

A considerable amount of work has been done by Blanchard and Blanchard, firstly using shock as a noxious stimuli and then exposure to a predator. The effect of brain lesions on SSDRs have also been examined.

Species-Specific Defense Reactions and Shock

Data supporting the notion of availability of escape determining which SSDR is prepotent has been found by Blanchard and Blanchard (1968). They suggested the competing SSDRs are pre-experimentally acquired and are elicited depending on the characteristics of the stimuli which elicited the fear. Blanchard and Blanchards' (1969a) finding that rats who had received shock did not 'crouch' if removed from the shock situation but increased crouching on return to the shock situation strongly suggests crouching is not a reaction to shock but is elicited and maintained by cues of the situation associated with shock. They argue that crouching

may be an index of fear. Further evidence supporting the importance of situational stimuli was found by Blanchard and Blanchard (1969b) when immobility appeared as a response to fear-eliciting situational stimuli. As neither immobility nor avoidance were similar to the unconditional responses, or reinforced by selective omission of further shocks, they concluded it was unlikely that they were solely operant in nature. The importance of situational stimuli is likely to govern which SSDR occurs - if the situation is poorly discriminated the whole situation elicits fear so immobility occurs, but a highly discriminable object quickly elicits avoidance (Blanchard and Blanchard 1970). They suggested at least two defensive reactions (active or passive) accompany pairing of a neutral stimulus with pain and this dichotomy of localised vs unlocalised threat is pre-experimentally acquired and has across-species generality.

The evidence on shock and SSDRs supports doubts about the assumption of equivalence of associability. Descriptive evidence of SSDRs occurring after shock have been found by Grossen and Kelley (1972) who found rats froze 12% of the time when unshocked compared with 82% when shocked. Further support for Blanchard and Blanchards' notion of fear being conditioned to situational cues was found in this study. When no specific conditioned stimulus was involved, immobility emerged rather than avoidance. Grossen and Kelley in a further experiment in the same paper observed that rats jumped onto a ledge on the side of a box rather than onto one in the centre of the box. Possibly, this was because the

former response more closely resembled an SSDR (running away).

Blanchard, Kelley and Blanchard (1974) found novel situations also elicit fear and a complex pattern of defensive reactions. Studies such as this one increased the generalizability of SSDR theory.

Blanchard, Fukunaga and Blanchard (1976) expanded further the notion of discriminability of situational cues determining the prepotent SSDR. They found that a brief familiarization period in a novel inescapable chamber made freezing the prepotent SSDR and suggested that exposure to the situation enabled the rat to discover that the situation was inescapable. They indicated similar results were found using using a predator instead of shock as a noxious stimulus.

Although the evidence on SSDRs and shock has clarified the importance of situational cues in determining the response, it has not avoided the circularity argument so the next expansion of SSDR theory occurred in the area of reactions to predators.

Species-Specific Defense Reactions and Predators

Since early this century there have been reports of fearful reactions to predators by small rodents and birds, particularly among wild animals. (Griffith, 1920; Kellogg, 1931).

Attempts to isolate the critical factors in this behaviour suggested that movement was important rather than odour or vision alone (Curti, 1935, 1941). Curti found some evidence of dependence of the response on the situation. In an earlier statement of part of SSDR theory she says

> "when there are no restraining objects, active flight occurs; in a small space where any incipient move to flight would be instantly inhibited, the paralysis of fear occurs instead". p189.

However, she concluded there was no evidence of an innate fear response, finding much variability in reaction in laboratory animals.

In an experiment examining the reaction of woodrats toward snakes, Richardson (1940) suggested response to the snake stimulus was inherited, developing by maturation. The sight, sound, movement and odour of snakes were required to produce the reaction - less than this configuration being insufficient to produce fear.

All these early studies were quasi-experimental and poorly controlled, with no statistical analyses done on their results, so caution must be observed when interpreting their results. In some cases handling was confounded (Curti 1941), pain was confounded with fear (Curti, 1935), and in others conclusions unfounded on any empirical evidence were drawn.

Studies on reaction to predators did not become 'fashionable' again until the early 1970s when Blanchard and Blanchard (1971) investigated SSDRs in a naturalistic setting. Their earlier experiments with shock were then re-examined and predators took the place of shock as noxious stimuli. They concluded that the rapidity of development and specificity of the responses to threat, represent Bolles' (1970) SSDRs. In a variety of apparatus and using different stimulus animals, Blanchard and Blanchard found either

difficulty in finding an appropriate control for the predator; a difficulty that was also experienced in the present study. Further discussion of this problem can be found in Chapter 4.

Further research examined what stimulus characteristics were important in eliciting SSDRs (Blanchard, Mast and Blanchard, 1975). These authors found that auditory stimulus of cat vocalization alone was not sufficient to produce reliable defensive responses, nor odour alone. Sight of a cat increased freezing however, and this was enhanced if the cat was moving. A moving card produced variable responses which were not as strong as those produced by the predator. They concluded that movement is important although some types of movement are more important than others. Stimuli resembling a natural predator acquired control more quickly over conditioned emotional responses. Movement appeared important for the initiation of freezing but other factors were important for its maintenance. This is consistent with work done by Curti (1935). Other animals (e.g. a dog) were found to elicit SSDRs also.

Bronstein and Hirsch (1976) examined the ontogeny of defensive reactions and found young rats did not show good passive avoidance learning (20 day olds being unresponsive to footshock, predators or a moving object). However, weanlings were able to associate a specific taste with illness, supporting the idea of two separate defense systems - one to do with external threats and the other with internal. The age at which most nutrition comes from extra-maternal sources corresponds with development of ability to learn this taste association and at the age (30-40 days) when exposure to

predators is more likely, the defensive reaction of freezing occurs. They suggested the development of the hippocampus may be necessary for responsiveness to external threat.

This group of studies provides clear evidence that predators elicit freezing or flight SSDRs in rats and that this is pre-experimentally acquired with maturational factors being important. The predator stimulus is unambiguous and tends to elicit avoidance (if this is possible) rather than immobility which is more likely to be elicited if the situational cues are less clear or escape is impossible.

Species-Specific Defense Reactions and Brain Lesions

There is some evidence that the limbic system of the brain is involved in species preservation and self-preservation (MacLean, 1958; Valzelli, 1973). In particular, the fronto-temporal zone of the limbic system (especially the hippocampus) is thought to be concerned with attack, defense and nutrition.

There is some evidence also that the effect of hippocampal lesions is to disrupt immobility reactions to threat (Blanchard and Blanchard, 1972b; Blanchard, Blanchard and Fial, 1970; Thomas, Hostetter and Barker, 1968).

However, it is unlikely that these effects can be explained as deriving solely from lesion induced alteration in any one defensive disposition (Thomas et al., 1968).

Lesions of the hippocampus, septum and cingulum have been found, respectively, to result in less crouching and poorer passive avoidance, less crouching with passive avoidance unchanged, and poorer passive avoidance with crouching unchanged (Blanchard and Fial, 1968) when threatening stimuli

are presented. They suggested the effects of these lesions may be a disruption of immobility by hippocampal lesions. Further evidence for disruption of defensive immobility reactions has been found by Blanchard, Blanchard and Fial (1970) who concluded a central mechanism for immobility exists which is different from that which controls avoidance. There are three possible reasons for the results on hippocampal lesions postulated by the authors above: (i) the Hippocampus is involved in the association of neutral and noxious stimuli. If this explanation is correct, experiments involving unconditioned fear (e.g. reactions to a predator) should not result in disruption of immobility. However, Blanchard and Blanchard (1972b) found immobility was disrupted in the presence of a cat. This explanation thus cannot be used to explain disruption of immobility. (ii) Hippocampal animals have higher pain thresholds than controls. However, Blanchard and Fials' (1968) results dispute this explanation as hippocampal damage did not increase shock thresholds for flinch or jump reactions. (iii) Hippocampal rats may be deficient in emotional reactions involving immobility.

Studies examining the effect of brain lesions on the rats' reactions to a cat provided further evidence for the importance of both the hippocampus and the amygdala in defensive reactions. Kim, Kim, Kim, Kim, Chang, Kim and Lee (1971) found in the presence of a cat both controls and hippocampal animals consumed less, were less active and avoided the cat, but hippocampal animals were 'bolder'. They concluded the hippocampus may have mechanisms that facilitate

emotional activity in both fear and aggression. Blanchard and Blanchard (1972a) found animals with both extensive and restricted amygdaloid lesions showed reduced freezing to an immobile cat and to a previously neutral stimuli associated with shock, and increased approach to the cat and shock prod. This means the altered SSDRs cannot be accounted for as a deficit in sensory modality or attentiveness nor as motor inhibition, because they approached more than controls. Associations between neutral and noxious stimuli were not disrupted as both conditioned and unconditioned stimuli elicited similar results. They suggested the amygdala is involved in regulation of the emotional-motivational state necessary for SSDRs, and possibly the deficits produced by amygdaloid lesions are mediated by a 'negative affect' state regulated by the amygdala.

Reactions by hippocampal animals to a predator (cat), result in lower freezing but superior avoidance (Blanchard and Blanchard, 1972b). They found more striking evidence of disruption by hippocampal lesions than Kim et al. (1971) and concluded that the effects of hippocampal damage may be mediated by altering innate freezing reactions.

Procedures involving brain lesions have elucidated the role of central processes in SSDRs to a limited extent. However, as the limbic system and the neocortex are extensively interconnected, there is unlikely to be a clear division of labour so that the former mediates innate behaviour and the latter, learned behaviour (Thomas et al., 1968).

Some drugs, especially compounds active on the limbic system, may clarify the existing confusion over the role of central processes in SSDRs. Similarly, examination of drugs in a situation independent of avoidance conditioning while still evoking fear, avoids confounding of effects with learning-memory mechanisms.

Only two studies have used drugs to modify rats' reactions to a predator. Plotnik, Mollenauer and Snyder (1974) investigated the effects of scopolamine on SSDRs. This well-controlled study demonstrated significantly less freezing and more approach and feeding behaviour in drugged animals. Methyl-scopolamine (which mimics the peripheral action of scopolamine) had no effect on fear responses, indicating a central cholinergic system is involved in mediation of SSDRs. They suggested a possible reason for attenuation of fear or defense responses was that blockage of olfactory cues occurred. However, Plotnik et al. (1974) did not refer to early work done by Curti (1935) that suggested olfactory cues alone were not critical for fear responses to occur. Subsequent work by Blanchard, Mast and Blanchard (1975) provided further evidence that olfactory cues do not play a major role. Mollenauer, Plotnik and Southwick (1976) subsequently reported that the drug did not affect fear or defense responses through actions on olfactory perception. Scopolamine was found to affect fear responses to a stimulus that did not involve smell (a robot). This stimulus was found to evoke fear responses thus enhancing generalizability of the finding that scopolamine affects defense reactions (Mollenauer et al., 1976). Conclusions about sites of action of scopolamine are limited as there is

debate over the manner in which it acts. Such consideration is beyond the scope of this study. However, there are numerous demonstrations of anticholinergic drugs affecting behaviour in a similar manner to that of bilateral removal of the hippocampus (Douglas and Isaacson, 1966).

Drugs affecting the limbic system without having anti-cholinergic effects may also disrupt SSDRs, although speculation about the sites of action of these drugs is sometimes limited by lack of understanding of their neurological effects. Chlordiazepoxide was chosen as the compound for study in the present experiment, in order to observe whether it modifies the rats' reactions to a predator.

Chlordiazepoxide (Librium)

Research in the late 1950s isolated a new class of compounds called the benzodiazepines, of which chlordiazepoxide (Librium) is the first member.

This drug has been found to have taming effects in septal animals (Christmas and Maxwell, 1970; Garattini, Mussini and Randall, 1973; Gordon, 1964; Randall, 1961; Schallek, Kuehn and Jew, 1962), anti-anxiety effects in humans (Garattini et al., 1973; Heise and Boff, 1961; Randall and Kapell, 1961; Tobin and Lewis, 1960), anti-convulsant activity (Randall, 1961), appetite stimulation (McDonald, Stern and Hahn, 1963; Root and Hofman, 1965), muscle relaxant effects at low doses and sedative effects at high doses (Randall, 1961). The drug is characterised by lack of hypnotic effects at the muscle relaxant level, strychnnine blocking and spinal reflex blocking (Randall, 1960b). It lacks

autonomic blocking effects and moderate doses have no effect on blood pressure or heart rate. The drug is extremely well tolerated in chronic administration (McDonald et al., 1963; Randall, 1961) and there is no evidence for deleterious influence of chlordiazepoxide on reproduction (Randall, 1960a).

There has been much work done on behavioural effects of chlordiazepoxide administration, with effects on spontaneous activity, preference for novelty, rearing, avoidance and escape, being reported. This will be quoted, where relevant, in relation to the results of this study, in a later section.

The sites of this drug's action in the brain are not well understood. However, depressant effects on the limbic system have been found after administration of chlordiazepoxide. Typically, there is significant slowing of electrical activity in the septum, amygdala and hippocampus, but not in the neocortex (Heise, 1965;Schallek, Kuehn and Jew, 1962; Zbinden and Randall, 1967).

Specifically, chlordiazepoxide has been found to attenuate hippocampal response, depressing after discharge without impairment of arousal (Domino, 1962; Himwich, Morillo and Steiner, 1962; Valzelli, 1973).

Disruption of hippocampal theta rhythm occurs after drug administration but a number of competing hypotheses exist to explain the function of theta rhythm. Grastýan, Lissák, Madárasz and Donhaffer (1959) suggested the normal function of the hippocampus is to inhibit the orienting response to insignificant sensory stimuli and when theta is present and accompanied by orienting, the hippocampus is inactive. However, Adey, Dunlop and Hendrix (1960) said theta may signal the active involvement of the hippocampus in the

processing, storage, and recall of information. While this debate remains unresolved, interpretation of chlordiazepoxide's effect on depressing theta rhythm is not possible.

Some authors suggested chlordiazepoxide exerts differential action on the amygdala and hippocampus. The electrical activity of the amygdala and hippocampus are depressed which results in the amygdala becoming less reactive and the hippocampus more reactive (Himwich et al., 1962; Schallek, Zabronsky and Kuehn, 1964; Zbinden and Randall, 1967). If depression of the hippocampus enhances reactivity, this would tend to support Grastýan et al.'s (1959) theory.

Neurotransmitter levels do not appear to be affected by chlordiazepoxide, although recent evidence suggested there may be small effects in turnover of these substances. Taylor and Laverty (1973) found decreases in norepinephrine turnover in the thalamus, hypothalamus, midbrain cortex and cerebellum regions, and decreased dopamine turnover in the corpus striatum. Possibly the role of neurotransmitters has been overlooked in the past because the size of effects is small and they are selectively localized (Lingjaerde, 1973; Gottschalk, Noble, Stolzoff, Bates, Cable, Uliana, Birch and Fleming, 1973; Valzelli, 1973).

The cortex does not appear to be affected by drug administration but interconnections between the limbic system and the cortex are extensive and some effects may be mediated there.

Hippocampal theta rhythm has been found to be important early in conditioned avoidance training when novelty responses of orienting and freezing prevail (Sachs, Weingarten and Klein, 1966). Hippocampal lesions disrupted immobility responses (see the previous section). Thus, if the drug does depress hippocampal electrical activity, disruption of both immobility and avoidance responses to threat may be expected to occur. Whilst confusion exists over the function of the hippocampus and the central action of chlordiazepoxide, interpretation of results of drug action on SSDRs in the light of the central nervous system would be at best suggestive. It was decided, after consideration of this literature, that interpretation of results found after chlordiazepoxide administration, should be descriptive rather than interpreting central activity. Some possible mechanisms will be suggested, however.

Other Considerations

Very little attention has been paid to sex differences in psychological research, most studies using either males or females without considering whether their results are sex dependent. It has been shown that factors such as sex are important in determining results of psychotropic drug administration (Irwin, Slabok and Thomas, 1958; Hughes and Syme, 1972). Variable results found in many drug studies may be partially the result of lack of attention to important variables such as this. In the present study, both males and females were included to allow for examination of sex dependent effects.

Housing of animals may also be important, (Archer, 1969; Hughes and Syme, 1972). Most studies do not report whether the animals were housed singly or in groups which suggests this is either not considered important or is ignored. As group housing more closely approximates the natural conditions that wild rats live in, it was decided to house the animals for this study in groups. Other relevant studies which did report housing used individual housing, however (Blanchard and Blanchard, 1971; Blanchard and Fial, 1968; Blanchard, Kelley and Blanchard, 1974; Plotnik et al., 1974).

Early handling has also been found to be important. Unhandled animals are more emotional in novel situations than handled animals (Denenberg, 1964; Levine, Haltmeyer, Karas and Denenberg, 1967). Many studies omit to report the handling history of their subjects and thus make it difficult to compare their results. Persistence, in general psychology, in ignoring important developmental variables, means that extraneous bias is introduced into many otherwise good designs.

Usually, in psychological research, one strain only of animals is used. There has been some research done on strain differences which has been suggestive in that albino rats appear to be more 'emotional' than hoodeds in many situations. (Hughes (1973) found albinos spent more time motionless than hoodeds and Carr and Williams (1957) found hooded rats explored more than albinos.) Most of the studies relevant to this research used albinos, so it was felt generality of results could be extended by also using hooded rats.

Many measures of emotionality have been found to be inadequate (Archer, 1973). Archer (1973) suggested a single emotionality drive concept is not useful and a complex of factors may be more useful in examining fear. Rather than depending on one or two measures of SSDRs, several measures may reveal which criteria best measure SSDRs. Other studies in the SSDR area have relied on a few measures to demonstrate the effect of unconditioned noxious stimuli. Blanchard and Blanchard (1971) used two measures to assess freezing: locomotion times and lines crossed. This was a somewhat gross measure of freezing as absence of lines crossing and locomotion does not necessarily imply freezing. It was felt that freezing would be better examined by actually defining it, rather than assuming that freezing was occurring in the absence of lines crossing and locomotion. Also, it was felt to be important to distinguish between freezing and immobility due to the considerable confusion in the literature over what exactly constitutes freezing. Other more recent unpublished work is now also using a time-sampling method and distinguishing between freezing and immobility. Fukunaga (personal communication) defined two states: freezing (corresponding to immobility in this study) and absolute freezing (equivalent to freezing in this study).

Blanchard and Blanchard (1971) recorded avoidance if the rat turned away from the predator or backed more than one-half an alley segment. For each avoidance response they measured distance between the subject and the predator and lines crossed. Approach to the cat was also recorded. Escape

or 'avoiding' the predator was also measured differently in this study so that latency to leave the vicinity of the predator and distance from the predator were measured. Other criteria such as grooming and rearing were included in the present research so that some statement could be made about the effect of a predator on types of activity rather than just activity or lack of it.

In order to expand generalization, a ferret was used as a predator in this research. Ferrets have traditionally been used for ratting (Faris, 1950) and were expected to act as a predator.

1.3 NATURE AND SCOPE OF THIS STUDY

Research Rationale

A review of the literature has revealed the necessity for further study of SSDRs in naturalistic settings. The SSDR concept appears to be a useful one, and examination of SSDRs should generate some interesting information. Use of the SSDR concept when examining reactions to threat does not necessarily imply acceptance of all the implications or assumptions of SSDR theory, however.

Attempts to identify the sites in the brain concerned with release and maintenance of SSDRs are also important. Clearly, the limbic system is involved in species and self preservation as well as emotional activity, and appears to be important in SSDRs.

Chlordiazepoxide has been shown to affect electrical activity of the limbic system and could be expected to modify reactions to threat. A dose lower than that causing sedation was chosen for this research, in order to minimize the effects on motor activity.

Several improvements on other designs were incorporated into the design. Generality of results were enhanced by the use of two strains of rats, a different predator to those used in other research, and inclusion of both sexes of subjects. An attempt was made to more adequately define dependent variables and a wide range of measures was employed. Larger numbers of subjects were included in this study and a powerful method of analysis was used on the results.

In summary, this study undertook examination of two strains of rats' reactions to a ferret. Chlordiazepoxide or distilled water was administered and results were measured by a wide range of dependent variables.

Research Questions

The major research question to be answered was: do rats react differently in the presence of a predator as opposed to a control rat, as measured by the present dependent variables?

Subsidiary questions concerned the effect of chlordiazepoxide administration on SSDRs and the role of strain and sex in responses to threat.

The adequacy of the present dependent variables in measuring SSDRs was also of interest.

Research Expectations

A number of relationships were predicted from the literature.

Presence of the predator was expected to increase freezing and immobility but reduce time spent in close proximity to the stimulus animal. The latter was expected to be expressed by more time spent in the far end of the apparatus and faster latency to leave the vicinity of the stimulus animal.

Response competition was not expected. The availability of escape was expected to render escape prepotent over freezing.

Drugged animals were expected to show modified reactions, the direction of which was not predicted.

CHAPTER 2

METHOD

2.1 SUBJECTS

The subjects were 48 black and white New Zealand Hooded rats and 48 albino rats of the Wistar/Sprague Dawley strain, with equal numbers of males and females.

They were housed in plastic cages, 45 cm long x 27 cm wide x 18 cm high, in single sex groups of 3-4 per cage. Food and water was freely available at all times.

Temperature in the animal house was kept at a constant $70^{o}F$ and the room was under a reversed light-dark schedule.

All the animals were naive, with no auditory, visual or olfactory experience with the predator (ferret) prior to experimentation.

The rats were handled daily prior to weaning at twenty-one days, and thereafter in an unsystematic fashion. However, the Wistar rats were brought into the laboratory at 21 days and may have received less early handling than the Hooded rats.

All the animals were weighed prior to experimentation, (Table 1).

Table 1. Average Weight in Grammes at Experimentation

	Wistars	Hoodeds
Males	378 (range 325-425)	390 (range 340-441)
Females	248 (range 215-275)	219 (range 181-237)

2.2 STIMULUS ANIMALS

The Predator

A young female New Zealand ferret (Mustela furo) served as the predator. Her diet consisted of dog sausage, milk, and water which she was fed in the evening after the completion of experimentation. She lived in quarters completely apart from the rat colony, in a wooden, straw-lined cage with another female ferret. She was naive, having had no prior experience with rats or any other small animal or bird.

The Predator Controls

Rats of the same strain and sex as the experimental animals served as controls for the ferret, the same stimulus rat being used for all the subjects in a condition. They were not cage mates of the experimental animals but were housed in similar conditions.

2.3 APPARATUS

The apparatus consisted of an arena with a perspex enclosure attached to an inner wall of the arena, and a runway extending from the outside of this wall (see Figure 3).[1]

This apparatus can be conceived as being in two separate parts, one being for the stimulus animals (the arena with the exception of the perspex enclosure) and the part for the experimental animals (the runway and the perspex enclosure), neither group of animals being able to come into actual physical contact.

1. Appendix 3 contains photographs of the apparatus and animals.

Two identical, square wooden boxes served as arenas (dimensions: 60 cm x 60 cm x 43 cm), one being used for the ferret and one for the non-ferret controls. A small door in the back wall of each arena provided entrances for the stimulus animals and the lid of each arena was made of perspex.

The perspex enclosure, with dimensions of 20 cm x 25 cm x 18 cm, fitted over a square hole in the end wall of the arena, forming one portion of the runway. This enclosure had holes in one end, allowing olfactory, auditory and visual cues to come from the stimulus animal in the arena (see Figure 5).

The runway was attached to the outside of the arena, over the square hole, thus joining up with the perspex enclosure, and a guillotine door divided the two structures. The runway was made of grey metal with dimensions of 20 cm x 100 cm x 30 cm, the length being divided into four equal portions by means of three small wooden hurdles (1 cm high). The lid of the runway was made of strong wire-mesh and this lid was able to be raised to place the experimental animals in the apparatus (Figure 4).

Two 22 watt fluorescent lamps provided illumination and these were positioned as indicated in Figure 2.

A white noise generator was used to mask extraneous noise from other parts of the laboratory.

An electric timer signalled a beep every four seconds, the beep having a duration of 0.3 of a second.

A stop watch was used to record time and a hand operated counter was used to record hurdles crossed.

FIGURE 2. LOOKING DOWN ONTO THE APPARATUS

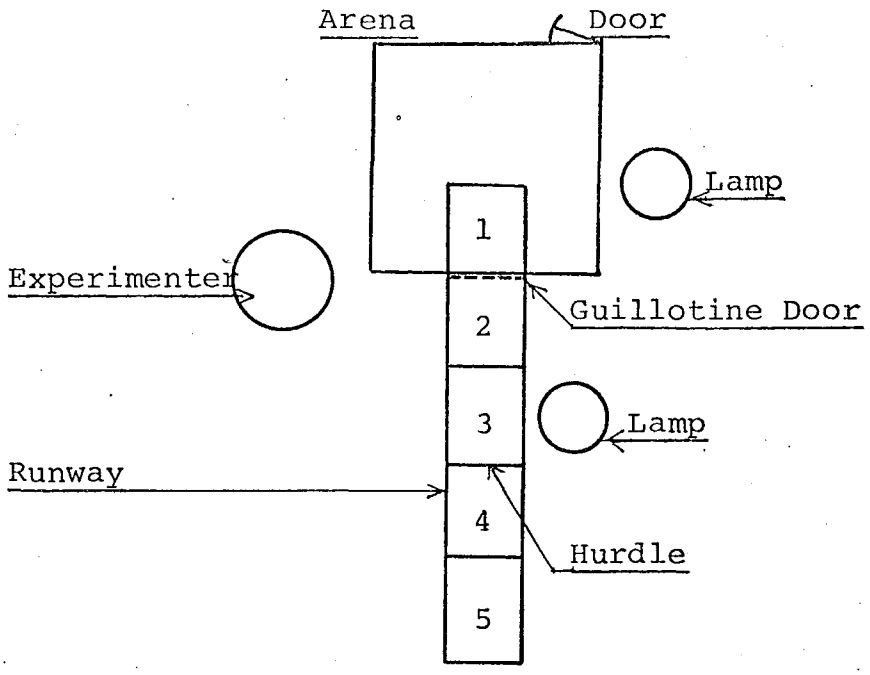


FIGURE 3. THE APPARATUS VIEWED FROM THE SIDE

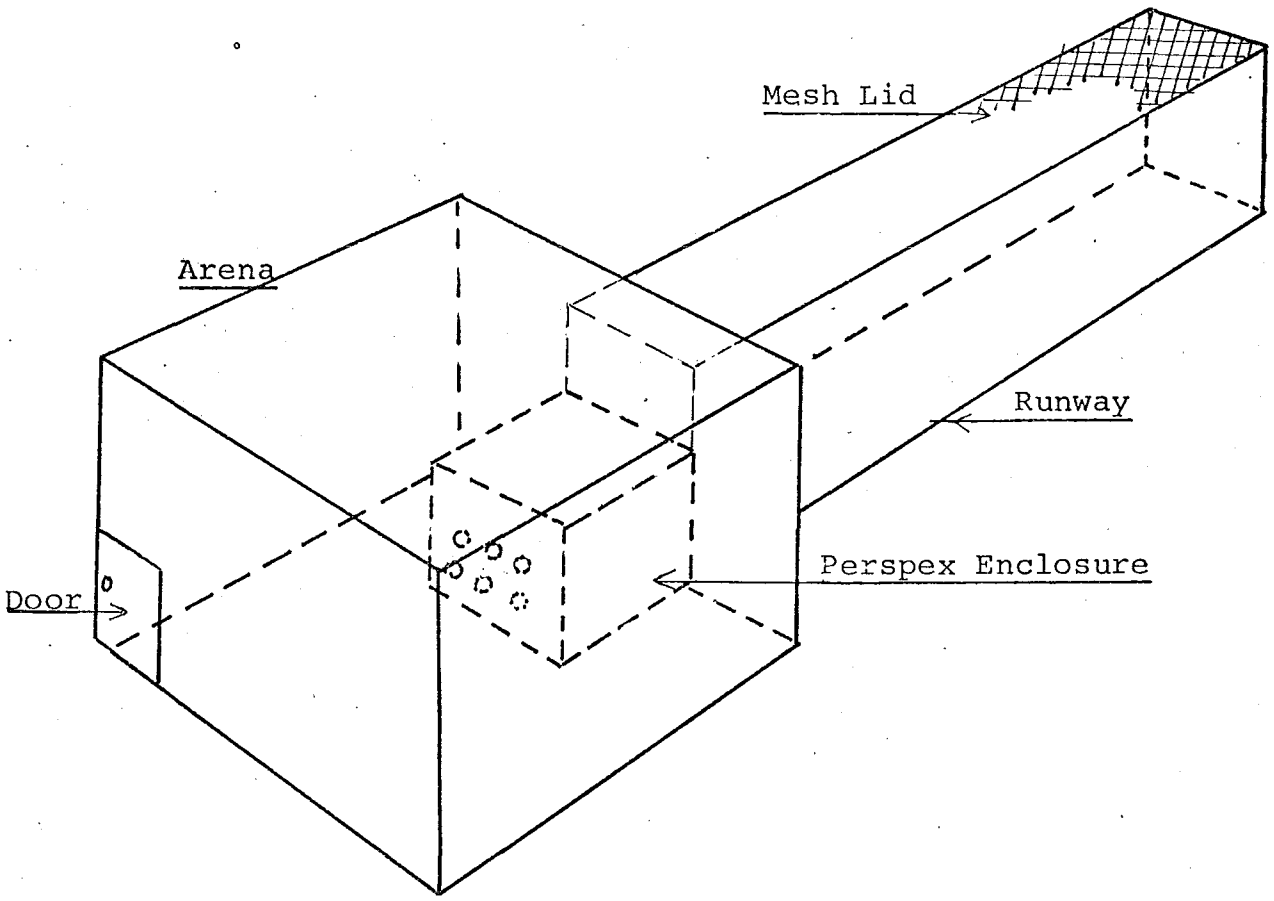


FIGURE 4. THE INSIDE OF THE RUNWAY

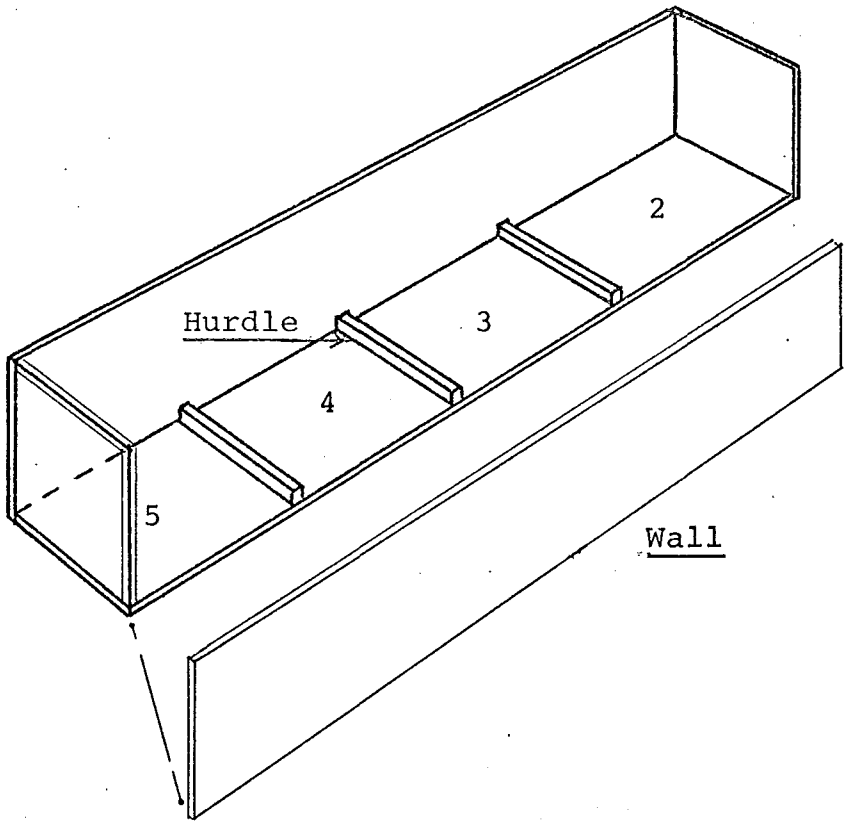
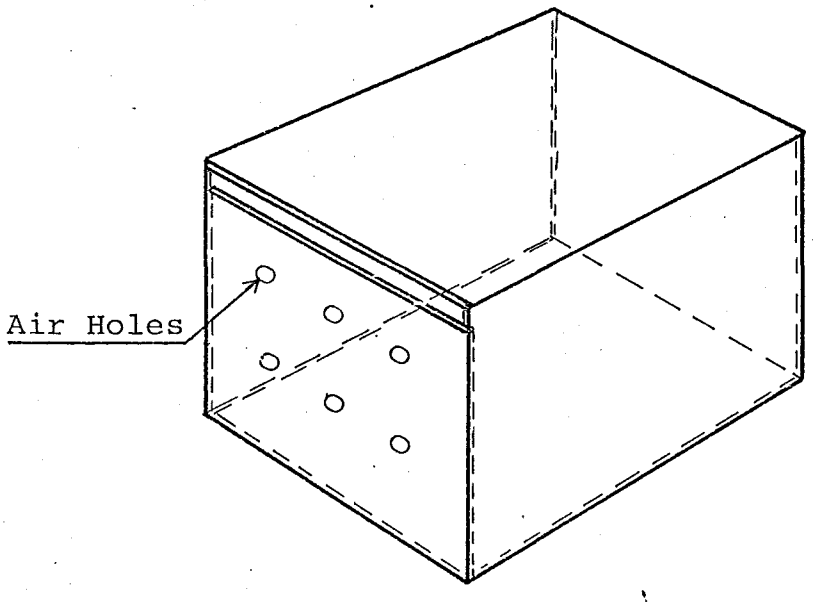


FIGURE 5. THE PERSPEX ENCLOSURE



The experimenter sat on a stool in the position marked on Figure 2; this was on the end corner of the arena overlooking the runway and perspex enclosure.

2.4 PROCEDURE

1. Dependent Variables

Four types of measures were taken during the experiment; a time sampling method being used for all except the latency and the activity measures.

(i) Latency: This was time taken to move from the perspex enclosure (or start box) and was measured in multiples of four seconds.

(ii) Cell: The second measure was the animal's location in the runway when the beep sounded; the cell in which the animal's hind feet were in being the cell recorded. The start box was Cell 1, and the opposite end of the runway was Cell 5.

(iii) Activity: General activity was measured by counting every time the animal's hind legs went over a hurdle. This was totalled every 40 seconds and at the conclusion of the observation period.

(iv) Categories of General Behaviour: The final measures were seven categories, one of which was recorded every four seconds when the beep sounded. A modified version of Bindra and Blond's (1958) time-sampling method was used (see Table 2). The categories are mutually exclusive and in hierarchical order so that if there was a conflict over which behaviour to record, the one higher up the list was recorded.

Table 2. Definitions of the Categories of General Behaviour[1]

Name	Definition
1. Grooming	Rat licks, scratches, or cleans any part of its body.
2. Locomotion	Rat moves on all four limbs - includes walking or running but not moving on rear legs.
3. Rearing	Rat raises itself so that it is supported by its hind legs only.
4. Sniffing	Rapid movement of the whiskers, usually accompanied by nose twitching, neck stretching, and the sound of sniffing.
5. Immobility	Complete cessation of all movement except for the whiskers.
6. Freezing	Complete cessation of all movement except for movements associated with breathing.
7. Approach-Avoidance	Rat stands over a hurdle making moves to enter another cell and then withdrawing. This 'hovering' is usually done with the front portion of the body. Record if animal is withdrawing immediately after attempting to enter a new cell.

Table 3. Assignment to Conditions

Strain:	Hoodeds		Wistars	
	Drug Control	Drug	Drug Control	Drug
Predator				
F	6	6	6	6
M	6	6	6	6
No Predator				
F	6	6	6	6
M	6	6	6	6
	Σ24	Σ24	Σ24	Σ24
		Σ48		Σ48

Note: M=male F=female

1. Much of the method and dependent variables used here were the result of an initial pilot study.

2. Assignment to Conditions

Two weeks prior to experimentation, each cage of rats was randomly assigned to a condition, to form eight conditions for each strain, See Table 3.

Also one week prior to experimentation, each animal was marked with an aerosol spray dye so that they could be readily identified.

3. Experimentation

The experiment required two days to complete each condition, the first day being habituation and the other being the data collection day. There was random assignment of the order in which conditions were done, all six animals in each condition being run on the same day. Within each condition there was random assignment of the order in which the animals were tested.

Day 1: Each rat was habituated to the apparatus within 24 hours of testing. The procedure for habituation was the same as for Step B of Day 2 except that no stimulus animals were in the arena and no data was recorded.

The stimulus animals were also habituated to the apparatus and experimenter prior to testing.

Day 2: On testing days the stimulus animals were placed in the arena of the apparatus at least 30 minutes before the experimental animals were placed in their part of the apparatus.

Step A: Each animal was weighed and then injected intraperitoneally with either the drug or drug control adjusted to its body weight.

Subjects in the drug condition were injected with Chlordiazepoxide (Librium) dissolved in distilled water at a concentration of 4 mg/ml and at a dose of 4 mg/kg, and the

drug control subjects with an equivalent volume of distilled water. Both groups were returned to their home cages for 30 minutes after injection and then were tested.

Step B: For testing, the subject was taken into the testing room and placed in the perspex enclosure and confined there for 30 seconds by means of the guillotine door. The door was then raised and the animal's behaviour recorded as outlined previously, for eight minutes, after which the animal was returned to its home cage.

CHAPTER 3

RESULTS

3.1 INTRODUCTION TO THE ANALYSES

Statistical analyses of the data were carried out using a multivariate analysis of variance programme (MANOVA)[1]. This is a flexible and powerful technique allowing unlimited re-analyses and performing univariate and multivariate analyses of variance, of covariance, and regression.

The design factors and criteria and their abbreviations are as follows:

Design Factors: (Independent Variables)

			Levels
A: Strain	1	Wistar	2
	2	Hooded	
B: Sex	1	Female	2
	2	Male	
C: Predator	1	Predator	2
	2	No Predator	
D: Drug	1	Drug Control	2
	2	Drug	

Criteria: (Dependent Variables)[2]

FREEZ: Freezing

IMM: Immobility

GROO: Grooming

REAR: Rearing

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1. Devised by Dr Elliot Crammer of the University of North Carolina, and modified by Professor R.A.M. Gregson and Dr B. Davis to run on the Burroughs Computer at the University of Canterbury.

2. Defined in method section 2.4 Dependent Variables.

LOCO: Locomotion

SNIF: Sniffing

A-A: Approach-Avoidance

CELL 1

CELL 2

CELL 3

CELL 4

CELL 5

LXX: Lines Crossed

LAT: Latency.

Two different analyses of the data were undertaken.

Analysis 1: This was the main analysis of the data where all the dependent variables and factors were included.

Analysis 2: This analysis divided each criterion (except Latency) into three equal parts, each being 160 seconds in length. This enabled trends over time to be examined to see if there was consistency of behaviour over time.

3.2 ANALYSIS ONE

Table 4 presents the means and standard deviations of the smallest factorial groupings for each criterion.

The factorial design was complete with no missing cells and six observations per cell (except in one group which had five due to illness in one animal). Larger groupings of factors contained multiples of six observations; the main effects having 48 observations per cell.

Table 4. Within Cells Means and Standard Deviations

FACTOR A	B	C	D			VARIABLE FREEZ	IMM	GROO	REAR	LOCO	SNIF	A-A	CELL 1
1	1	1	1	6 OBS									
					M	0.167	35.833	2.333	10.667	43.333	26.000	2.500	21.500
					SD	0.408	3.430	3.266	3.615	7.367	6.812	2.168	15.897
1	1	1	2	5 OBS									
					M	0.400	46.800	6.000	9.800	40.000	15.800	1.200	22.400
					SD	0.894	26.574	8.689	6.760	11.402	4.438	1.304	36.315
1	1	2	1	6 OBS									
					M	0.000	6.333	3.333	42.500	31.833	36.000	0.000	66.333
					SD	0.000	6.121	2.582	10.578	5.193	4.940	0.000	22.923
1	1	2	2	6 OBS									
					M	0.000	12.667	3.333	38.167	37.167	28.667	0.000	59.333
					SD	0.000	13.397	2.338	9.704	7.574	9.416	0.000	12.754
1	2	1	1	6 OBS									
					M	0.000	10.333	5.500	16.667	49.667	36.500	1.333	5.333
					SD	0.000	12.596	6.804	7.312	3.204	8.735	1.966	5.715
1	2	1	2	6 OBS									
					M	0.500	40.000	4.833	11.833	35.833	25.667	1.333	32.833
					SD	0.837	28.093	9.948	12.937	6.047	6.890	2.422	20.262
1	2	2	1	6 OBS									
					M	0.000	14.667	6.667	25.667	38.667	34.333	0.000	69.000
					SD	0.000	24.262	3.077	13.456	15.161	4.457	0.000	24.116
1	2	2	2	6 OBS									
					M	0.000	14.000	4.500	38.500	30.000	33.000	0.000	68.167
					SD	0.000	15.153	1.517	10.464	7.772	10.178	0.000	21.236
2	1	1	1	6 OBS									
					M	0.000	6.667	0.667	23.500	32.000	51.500	5.667	13.833
					SD	0.000	6.861	0.816	10.950	8.695	11.946	1.633	10.265
2	1	1	2	6 OBS									
					M	0.167	6.833	3.167	32.167	34.667	42.167	0.833	26.667
					SD	0.408	6.113	1.602	7.305	4.179	6.338	1.329	19.755
2	1	2	1	6 OBS									
					M	0.000	3.167	7.000	41.833	26.000	42.000	0.000	56.500
					SD	0.000	2.927	8.602	14.851	8.173	12.231	0.000	15.643
2	1	2	2	6 OBS									
					M	0.000	8.333	6.000	41.667	26.333	37.500	0.167	79.667
					SD	0.000	9.309	4.858	13.292	9.004	8.068	0.408	20.530
2	2	1	1	6 OBS									
					M	0.000	7.167	11.333	19.333	34.000	45.000	3.167	18.333
					SD	0.000	2.401	10.132	9.309	5.621	10.257	3.430	9.288
2	2	1	2	6 OBS									
					M	0.000	19.333	2.833	17.500	38.500	39.500	2.333	23.500
					SD	0.000	14.922	3.817	9.333	4.846	12.341	1.751	12.292
2	2	2	1	6 OBS									
					M	0.000	1.667	3.333	50.167	28.333	36.500	0.000	55.167
					SD	0.000	1.506	1.366	7.360	4.546	5.167	0.000	8.377
2	2	2	2	6 OBS									
					M	0.000	2.000	4.000	32.667	40.000	41.333	0.000	57.333
					SD	0.000	2.280	2.191	7.711	6.132	9.522	0.000	11.466

Table 4 continued. Within Cells Means and Standard Deviations

FACTOR A	B	C	D			VARIABLE CELL 2	CELL 3	CELL 4	CELL 5	LXX	LAT
1	1	1	1	6 OBS							
					M	56.000	12.500	13.333	16.667	72.833	7.333
					SD	17.447	5.505	14.306	11.501	25.895	4.676
1	1	1	2	5 OBS							
					M	49.000	11.800	10.600	26.200	69.400	4.000
					SD	39.389	7.190	10.574	24.427	34.392	0.000
1	1	2	1	6 OBS							
					M	23.500	7.667	10.000	12.500	49.000	8.667
					SD	14.721	2.875	6.197	6.285	13.900	1.633
1	1	2	2	6 OBS							
					M	25.167	14.333	10.167	11.000	78.500	17.333
					SD	12.671	5.465	5.913	5.177	38.182	26.972
1	2	1	1	6 OBS							
					M	40.667	12.833	11.833	49.333	56.833	7.333
					SD	18.446	4.622	5.456	23.106	16.018	3.933
1	2	1	2	6 OBS							
					M	59.167	12.167	10.333	5.500	47.667	12.000
					SD	25.015	5.947	12.736	4.324	20.156	15.799
1	2	2	1	6 OBS							
					M	29.000	7.833	6.167	8.000	59.000	34.667
					SD	22.000	4.750	2.317	7.563	25.251	36.456
1	2	2	2	6 OBS							
					M	32.667	6.667	6.833	5.667	50.500	28.667
					SD	10.708	5.086	5.565	4.803	28.424	29.871
2	1	1	1	6 OBS							
					M	64.833	14.333	11.000	16.000	59.500	4.667
					SD	20.439	3.963	5.367	7.403	22.608	1.633
2	1	1	2	6 OBS							
					M	44.167	15.667	15.833	17.667	66.000	9.333
					SD	15.224	3.615	4.070	3.445	13.885	6.022
2	1	2	1	6 OBS							
					M	21.167	11.167	14.167	17.000	56.333	10.000
					SD	4.535	3.312	3.545	7.155	13.692	4.195
2	1	2	2	6 OBS							
					M	19.667	6.167	6.167	8.333	60.333	89.333
					SD	10.893	5.636	3.656	5.086	35.274	191.427
2	2	1	1	6 OBS							
					M	43.167	13.000	16.500	29.000	51.500	6.667
					SD	15.039	5.933	7.287	17.378	11.185	3.266
2	2	1	2	6 OBS							
					M	59.833	12.833	11.000	12.833	50.667	14.667
					SD	23.198	2.787	5.657	7.414	12.291	15.526
2	2	2	1	6 OBS							
					M	24.167	11.000	15.500	14.167	59.833	14.000
					SD	4.262	5.329	4.324	3.971	10.304	10.954
2	2	2	2	6 OBS							
					M	23.500	11.167	15.167	12.833	53.000	21.333
					SD	7.583	4.579	2.927	6.824	15.492	17.096

Table 5. Within Cells Correlations of Criteria with Standard Deviations on Diagonal

VARIABLE	FREEZ	IMM	GROO	REAR	LOCO	SNIF	A-A
FREEZ	0.325						
IMM	0.127	13.723					
GROO	-0.201	-0.251	5.425				
REAR	-0.092	-0.646	-0.052	10.141			
LOCO	-0.008	-0.494	-0.168	0.240	7.689		
SNIF	-0.003	-0.240	-0.004	-0.291	0.297	8.696	
A-A	0.007	0.026	-0.053	-0.163	0.052	-0.048	1.493
CELL 1	-0.136	-0.151	0.078	-0.005	0.119	0.153	-0.275
CELL 2	-0.101	0.369	-0.144	-0.291	-0.284	0.058	0.283
CELL 3	0.252	-0.309	-0.141	0.410	0.285	-0.178	0.104
CELL 4	0.092	-0.221	-0.105	0.308	0.167	-0.117	0.055
CELL 5	0.217	-0.080	0.241	0.106	0.037	-0.192	-0.023
LXX	0.001	-0.453	-0.041	0.412	0.346	-0.085	0.189
LAT	0.012	0.160	0.133	-0.157	-0.183	0.019	-0.051

	CELL 1	CELL 2	CELL 3	CELL 4	CELL 5	LXX	LAT
FREEZ							
IMM							
GROO							
LOCO							
SNIF							
A-A							
CELL 1	17.918						
CELL 2	-0.523	17.995					
CELL 3	-0.295	-0.243	4.897				
CELL 4	-0.386	-0.399	0.441	7.024			
CELL 5	-0.399	-0.425	0.153	0.451	10.884		
LXX	-0.101	-0.260	0.406	0.443	0.129	22.690	
LAT	0.323	-0.167	-0.178	-0.124	-0.096	0.289	50.693

Table 5 presents the within cells correlations of criteria with the Standard Deviation of each variable on the leading diagonal. There were no high correlations but a number of moderate ones. As could be expected, Immobility was negatively correlated with Rearing (-0.646), Locomotion (-0.494) and Lines Crossed (-0.453). Immobility was positively correlated with Cell 2 (0.369) demonstrating an association between presence in Cell 2 and immobility.

Rearing was positively correlated with Lines Crossed (0.412) and with Cell 3 (0.410), indicating a moderate relationship between general activity and amount of rearing and between presence in Cell 3 and rearing.

Locomotion also had a low positive correlation with Lines Crossed (0.346) which demonstrates that animals who were more active generally also moved about more within each cell. This was expected, as in order to move over a wide area of the apparatus the subjects had to move within each cell (although not necessarily vice versa).

Lines Crossed and Cell 4 were positively correlated (0.443) and Lines Crossed and Cell 3 (0.406). This indicates that crossing lines and being in Cells 3 and 4 occurred often together and this was also reflected in the low scores for presence in these cells. Animals were only in these cells on the way to either end of the runway.

Cell 1 had a moderate negative correlation (-0.523) with Cell 2, suggesting that animals who spent time in Cell 1 were less often in Cell 2. Other negative relationships existed between Cell 4 and Cell 2 (-0.399) and Cell 5 and Cell 2

(-0.425). There was also a low negative relationship between Cell 3 and Cell 2 (-0.243). Presence in Cell 2 appears to be negatively associated in a low or moderate manner with presence in other cells.

Cell 3 was positively correlated with Cell 4 (0.441) and Cell 5 was also positively correlated with Cell (0.406), indicating a moderate relationship between Cell 4 and the cells on either side of it.

All other correlations between criteria were low.

Table 6 shows a table of means for the significant main effects and interactions of each dependent variable. This table was derived from Table 4 and is the basis of the graphs reported below.

The results for this analysis are reported below by dealing with each main effect and interaction one by one.

A: Strain

The strain main effect resulted in a significant multivariate F test ($F = 9.325$ DF HYP[1] $= 14.00$ DF ERR[2] $= 66.00$ $P < .001$) with a high degree of multivariate association ($R = 0.815$) between the independent and dependent variables.

The standardised discriminant function equation for this strain main effect was:

$$V_{STRAIN} = 6.28(IMM) + 3.739(REAR) + 3.529(LOCO) + 3.116(SNIF) + 2.486(GROO) + 0.803(LXX) - 0.536(LAT) + 0.305(FREEZ) + 0.237(A\text{-}A) - 0.205(CELL\ 4) + 0.194(CELL\ 1) - 0.148(CELL\ 3) + 0.065(CELL\ 2) + 0.000(CELL\ 5).$$

1. DF HYP = Degrees of freedom associated with hypothesis.
2. DF ERR = Degrees of freedom associated with error.

Table 6. Means of the Significant Main Effects and Interactions[1]

	VARIABLE							
FACTOR	FREEZ	IMM	GROO	REAR	LOCO	SNIF	A-A	CELL 1
A_1	-	22.59	-	24.23	38.32	29.50	0.80	-
A_2	-	6.91	-	32.36	32.49	41.94	1.53	-
B_1	-	-	-	-	-	-	-	-
B_2	-	-	-	-	-	-	-	-
C_1	0.16	21.63	-	17.69	38.51	-	2.30	20.56
C_2	0.00	7.86	-	38.90	32.30	-	0.03	63.95
D_1	-	10.74	-	-	-	38.48	1.59	38.26
D_2	-	18.75	-	-	-	32.96	0.74	46.25
AB	Not Significant $p < .238$							
AC								
A_1C_1	-	33.25	-	-	-	26.00	1.59	-
A_1C_2	-	11.92	-	-	-	33.01	0.00	-
A_2C_1	-	10.01	-	-	-	44.54	3.01	-
A_2C_2	-	3.80	-	-	-	39.34	0.05	-
AD								
A_1D_1	-	-	-	-	40.88	-	-	-
A_1D_2	-	-	-	-	35.76	-	-	-
A_2D_1	-	-	-	-	30.09	-	-	-
A_2D_2	-	-	-	-	34.88	-	-	-
BC	Not Significant $p < .609$							
BD	Not Significant $p < .062$							
CD								
C_1D_1	-	-	-	-	-	-	3.17	-
C_1D_2	-	-	-	-	-	-	1.43	-
C_2D_1	-	-	-	-	-	-	0.00	-
C_2D_2	-	-	-	-	-	-	0.05	-
ABC								
$A_1B_1C_1$	-	41.32	4.17	10.24	-	-	-	-
$A_1B_1C_2$	-	9.51	3.34	40.34	-	-	-	-
$A_1B_2C_1$	-	25.17	5.17	14.26	-	-	-	-
$A_1B_2C_2$	-	14.34	5.59	32.09	-	-	-	-
A_2B_1C	-	6.76	1.92	27.84	-	-	-	-
$A_2B_1C_1$	-	5.76	6.50	41.76	-	-	-	-
$A_2B_1C_2$	-	13.26	7.09	18.42	-	-	-	-
$A_2B_2C_1$	-	1.84	3.67	41.42	-	-	-	-
$A_2B_2C_2$								
ABD								
$A_1B_1D_1$	-	-	-	26.59	37.59	-	-	43.92
$A_1B_1D_2$	-	-	-	23.99	38.59	-	-	40.87
$A_1B_2D_1$	-	-	-	21.17	44.17	-	-	37.17
$A_1B_2D_2$	-	-	-	25.17	32.92	-	-	50.51
$A_2B_1D_1$	-	-	-	32.67	29.00	-	-	35.17
$A_2B_1D_2$	-	-	-	36.92	30.51	-	-	53.17
$A_2B_2D_1$	-	-	-	34.76	31.17	-	-	36.76
$A_2B_2D_2$	-	-	-	25.09	39.25	-	-	40.42
ACD	Not Significant $p < .329$							

1. Only significant univariate results are reported here.

Table 6 Continued

FACTOR	VARIABLE FREEZ	IMM	GROO	REAR	LOCO	SNIF	A-A	CELL 1
BCD								
$B_1C_1D_1$	-	-	-	-	-	-	4.09	
$B_1C_1D_2$	-	-	-	-	-	-	1.02	
$B_1C_2D_1$	-	-	-	-	-	-	0.00	
$B_1C_2D_2$	-	-	-	-	-	-	0.09	
$B_2C_1D_1$	-	-	-	-	-	-	2.26	
$B_2C_1D_2$	-	-	-	-	-	-	1.84	
$B_2C_2D_1$	-	-	-	-	-	-	0.00	
$B_2C_2D_2$	-	-	-	-	-	-	0.00	
ABCD	Multivariate F test significant but no significant univariate F tests.							

FACTOR	VARIABLE CELL 2	CELL 3	CELL 4	CELL 5	LXX	LAT
A_1	-	-	9.92	-	-	-
A_2	-	-	13.17	-	-	-
B_1	-	-	-	-	63.99	-
B_2	-	-	-	-	53.63	-
C_1	52.11	13.15	-	21.66	-	-
C_2	24.86	9.51	-	11.19	-	-
D_1	-	-	-	20.34	-	-
D_2	-	-	-	12.51	-	-
AB	Not significant $p < .238$					
AC						
A_1C_1	-	-	-	24.44	-	-
A_1C_2	-	-	-	9.30	-	-
A_2C_1	-	-	-	18.88	-	-
A_2C_2	-	-	-	13.09	-	-
AD						
A_1D_1	-	-	-	-	-	-
A_1D_2	-	-	-	-	-	-
A_2D_1	-	-	-	-	-	-
A_2D_2	-	-	-	-	-	-
BC	Not significant $p < .609$					
BD	Not significant $p < .062$					
CD						
C_1D_1	-	-	-	27.76	-	-
C_1D_2	-	-	-	15.56	-	-
C_2D_1	-	-	-	12.92	-	-
C_2D_2	-	-	-	9.47	-	-
ABC						
$A_1B_1C_1$	-	12.15	-	-	-	-
$A_1B_1C_2$	-	11.01	-	-	-	-
$A_1B_2C_1$	-	12.51	-	-	-	-
$A_1B_2C_2$	-	7.26	-	-	-	-
$A_2B_1C_1$	-	15.01	-	-	-	-
$A_2B_1C_2$	-	8.67	-	-	-	-
$A_2B_2C_1$	-	12.92	-	-	-	-
$A_2B_2C_2$	-	11.09	-	-	-	-

Table 6 Continued

FACTOR	VARIABLE CELL 2	CELL 3	CELL 4	CELL 5	LXX	LAT
ABD						
$A_1B_1D_1$	-	-	-	14.59	-	-
$A_1B_1D_2$	-	-	-	18.60	-	-
$A_1B_2D_1$	-	-	-	28.67	-	-
$A_1B_2D_2$	-	-	-	5.59	-	-
$A_2B_1D_1$	-	-	-	16.50	-	-
$A_2B_1D_2$	-	-	-	13.01	-	-
$A_2B_2D_1$	-	-	-	21.59	-	-
$A_2B_2D_2$	-	-	-	12.84	-	-
ACD	Not significant $p < .329$					
BCD						
$B_1C_1D_1$	60.42	-	-	16.34	-	-
$B_1C_1D_2$	46.59	-	-	21.94	-	-
$B_1C_2D_1$	22.34	-	-	14.75	-	-
$B_1C_2D_2$	22.42	-	-	9.67	-	-
$B_2C_1D_1$	41.92	-	-	39.17	-	-
$B_2C_1D_2$	59.51	-	-	9.17	-	-
$B_2C_2D_1$	26.59	-	-	11.09	-	-
$B_2C_2D_2$	28.09	-	-	9.26	-	-
ABCD	Multivariate F test significant but no significant univariate F tests.					

This indicates that Immobility, Rearing, Locomotion, Sniffing and Grooming contributed most to the discrimination of the strain groups.

On the discriminant dimension used in the multivariate F test, the strain group means ($\bar{A}_1$ and $\bar{A}_2$) are represented as deviations (1.312 and -1.312 respectively) from the strain grand mean $\bar{A}$ which is set at zero. This could be represented diagrammatically but as there are only two levels of each factor such a representation would not provide any extra information. However, it can be noted that the larger the value of the discriminant scores contrast, the larger the difference between the two levels.

Univariate F tests resulted in six significant strain main effects.

Wistar rats were significantly more immobile than Hoodeds ($F = 29.013$ df = 1,79; $p < .001$). However, Hooded rats reared significantly more than Wistars ($F = 14.128$ df = 1, 79; $p < .001$). Wistars locomoted more often than Hoodeds ($F = 13.502$ df = 1,79; $p < .001$) and sniffed significantly less often than Hoodeds ($F = 46.357$ df = 1,79; $p < .001$). Approach-Avoidance occurred more frequently in Hooded animals than in Wistars ($F = 5.732$ df = 1,79; $p < .019$). Finally, Hooded rats spent more time in Cell 4 than Wistar rats ($F = 5.157$ df = 1,79; $p < .026$).

B: SEX

The sex main effect resulted in a significant multivariate F test ($F=1.87$ DF ERR = 66.00 DF HYP = 14.00 $p < .046$ $R = 0.533$). The standardized discriminant function equation for this sex main effect was:

V_{SEX} = 2.392(IMM) + 1.78(REAR) + 1.074(SNIF) + 1.023(LXX) - 0.615(LAT) + 0.601(GROO) + 0.486(CELL 1) + 0.407(A-A) - 0.335(CELL 4) + 0.313(LOCO) + 0.143(FREEZ) - 0.114(CELL 2) - 0.012(CELL 3) + 0.00(CELL 5).

This shows that Immobility, Rearing, Sniffing and Lines Crossed contributed the most to the discrimination between the sexes. On the discriminant dimension used in the significant multivariate F test, the individual treatment group means $\bar{B}_1$ and $\bar{B}_2$ are represented as deviations (0.572 and -0.572) from the sex grand mean $\bar{B}$ which is set at zero.

Univariate F tests produced only one significant result on Lines Crossed, with females crossing lines more often than males ($F = 4.876$ df = 1,79 $p < .03$) and as can be seen from the standardized discriminant function equation, Lines Crossed contributed to the multivariate discrimination.

C: PREDATOR

The predator main effect resulted in a significant multivariate test ($F = 21.735$ DF HYP = 14.00 DR ERR = 66.00 $p < .001$ $R = 0.907$). The standardized discriminant function coefficients were

$V_{PREDATOR}$ = 8.214(IMM) + 5.412(REAR) + 5.254(SNIF) + 5.128(LOCO) + 3.326(GROO) + 1.023(A-A) - 0.860(CELL 1) + 0.157(LAT) - 0.143(CELL 4) + 0.139(FREEZ) + 0.135 (CELL 3) - 0.123(CELL 2) - 0.037(LXX) + 0.00(CELL 5),

from which it is apparent that the dependent variables contributing most to the predator vs no predator discrimination were Immobility, Rearing, Sniffing, Locomotion, Grooming and

Approach-Avoidance. On the discriminant dimension used in the significant multivariate F test the group means $\bar{C}_1$ and $\bar{C}_2$ are deviations (1.959 and -1.959 respectively) from the predator grand mean $\bar{C}$ which is set at zero.

The univariate F tests resulted in the following significant effects and directions of effects.

Subjects in the predator condition were more immobile than those in the no predator condition ($F = 22.684$ $df = 1,79$ $p < .001$). Rearing occurred significantly less in the predator condition than in the no predator control ($F = 102.692$ $df = 1,79$ $p < .001$). Animals in the predator condition locomoted significantly more than those in the control condition ($F = 15.473$ $df = 1,79$ $p < .001$). Approach-Avoidance was more frequent in the predator condition than when there was no predator present ($F = 56.035$ $df = 1,79$ $p < .001$). Freezing occurred significantly more often in the predator condition ($F = 5.068$ $df = 1,79$ $p < .027$). Presence in Cell 1 was less frequent in animals in the predator condition than those in the no predator control ($F = 139.206$ $df = 1,79$ $p < .001$) and the reverse was true for Cell 2 ($F = 54.764$ $df = 1,79$ $p < .001$). Animals in the predator condition were significantly more in both Cell 3 and Cell 5 than animals in the control condition (CELL 3: $F = 13.305$ $df = 1,79$ $p < .001$ and CELL 5: $F = 21.497$ $df = 1,79$ $p < .001$). Latency approached significance with latency being greater for those in the control condition than for those in the predator condition ($F = 3.589$ $df = 1,79$ $p < .062$).

D: DRUG

The drug main effect resulted in a significant multivariate test ($F = 3.41$ DF HYP = 14.00 DF ERR = 66.00 $p < .001$ $R = 0.648$).

The standardized discriminant function coefficients were:

$$V_{DRUG} = -4.78(IMM) - 3.987(REAR) - 3.778(SNIF) - 3.057(LOCO) - 1.805(GROO) - 1.457(CELL\ 1) + 1.182(CELL\ 2) - 1.071(A\text{-}A) + 0.542(CELL\ 4) + 0.525(LXX) + 0.376(CELL\ 3) - 0.290(LAT) + 0.242(FREEZ) + 0.00(CELL\ 5),$$

from which it can be seen that Immobility, Rearing, Sniffing, Locomotion and Grooming contributed most to the multivariate discrimination. On the discriminant dimension used in the significant multivariate F test, the drug group means $\bar{D}_1$ and $\bar{D}_2$ are represented as deviations (-0.786 and 0.786) from the drug grand mean $\bar{D}$ which is set at zero.

Univariate F tests on five criteria were significant. Rats in the drug condition were immobile significantly more than those in the drug control condition ($F = 7.567$ df = 1,79 $p < .007$). Drugged rats sniffed less than undrugged animals ($F = 8.855$ df = 1,79 $p < .004$). Drugged rats engaged in Approach-Avoidance less often than those in the drug control condition ($F = 7.517$ df = 1,79 $p < .008$). Drug injected animals spent more time than controls in Cell 1 ($F = 4.820$ df = 1,79 $p < .031$) but drugged rats spent significantly less time in Cell 5 than drug control rats ($F = 12.895$ df = 1,79 $p < .001$).

INTERACTIONS:

AB: STRAIN X SEX

The multivariate F test of the two way interaction of strain x sex was not significant at the $p < .05$ level, and only one univariate test was significant: SNIF ($F = 5.185$ $df = 1,79$ $p < .025$).

AC: STRAIN x PREDATOR

The two way interaction of strain x predator resulted in a significant multivariate F test ($F = 2.27$ DF HYP = 14.00 DF ERR = 66.00 $p < .013$ $R = 0.570$). The standardized discriminant function equation for this interaction was as follows:

$$V_{AC} = 10.288(IMM) + 6.882(REAR) + 5.804(LOCO) + 5.730(SNIF) + 4.134(GROO) + 0.597(A\text{-}A) + 0.528(FREEZ) + 0.502(LXX) - 0.329(CELL\ 3) - 0.222(LAT) + 0.143(CELL\ 4) - 0.131(CELL\ 1) - 0.124(CELL\ 2) + 0.00(CELL\ 5).$$

from which it is apparent that the largest contribution to the multivariate discrimination was made by Immobility, Rearing, Locomotion, Sniffing and Grooming. On the discriminant dimension used in the significant multivariate F test, the contrasts are represented as deviations (0.640 and -0.640) from the AC interaction grand mean ($\overline{AC}$), which is set at zero.

Four criteria yielded significant univariate F tests.

Immobility: Figure 6 shows that the trend of the data for both strains was similar but there was a difference in absolute level between the strains. The rats in the no predator condition were less immobile than those in the predator condition. Wistar rats had a much greater level of

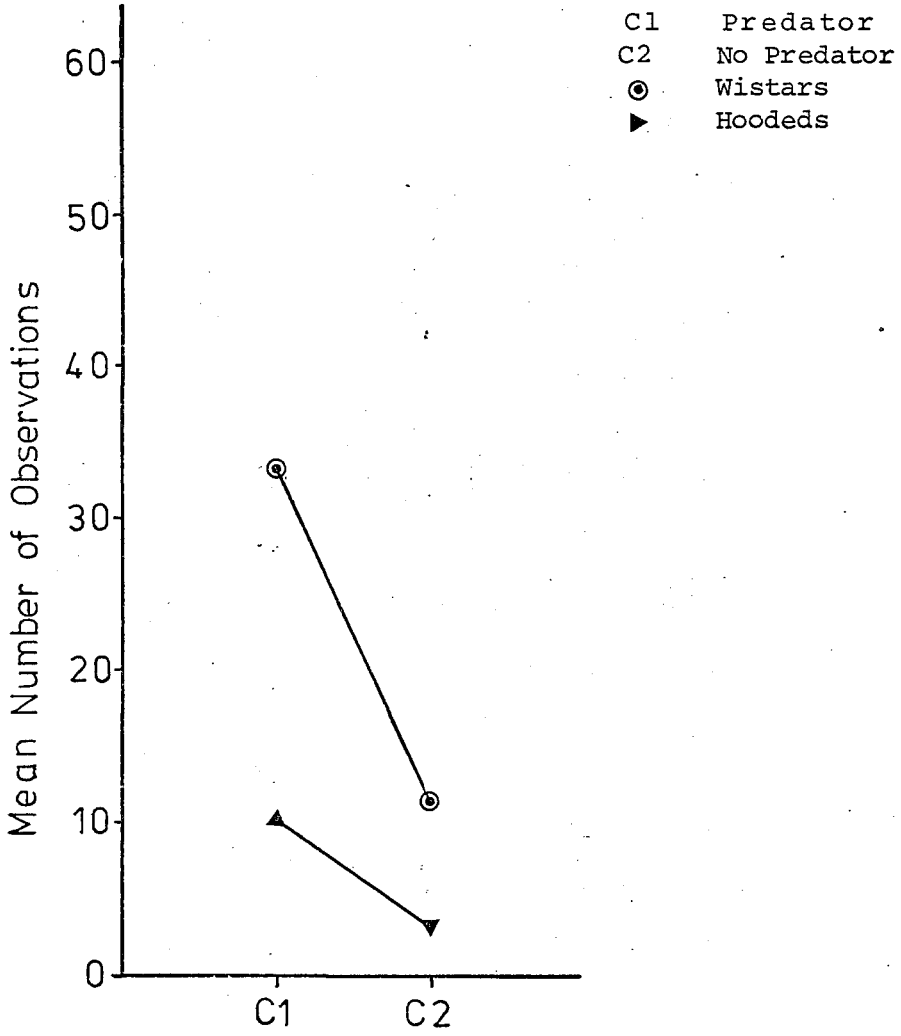

Figure 6 Immobility Scores for the Strain x Predator Interaction

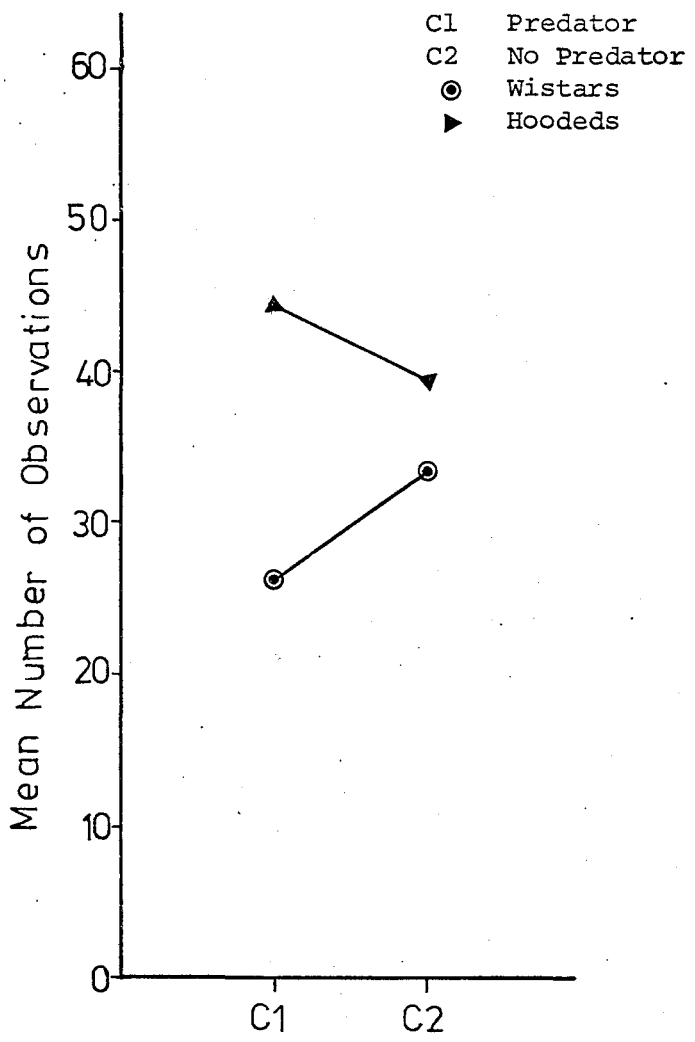

Figure 7 Sniffing Scores for the Strain x Predator Interaction

immobility than Hooded rats in both conditions, the amount of immobility in the predator condition for Hoodeds being similar to that in the Wistar no predator condition. The result was significant ($F = 6.915$ $df = 1,79$ $p < .01$).

Sniffing: Figure 7 shows that Wistars in the no predator condition sniffed less than Wistars in the predator condition and the reverse is true for Hoodeds. Hoodeds sniffed more than Wistars overall, the largest difference being in the predator condition. The univariate F test for Sniffing is ($F = 11.321$ $df = 1,79$ $p < .001$).

Approach-Avoidance: Figure 8 shows that the trends for both Wistars and Hoodeds were similar - both strains showed greater Approach-Avoidance in the predator condition than in the no predator condition. However, Hoodeds showed more approach-avoidance generally than Wistars. In both strains a very low level of approach-avoidance was observed. The univariate F test for approach-avoidance is ($F = 4.939$ $df = 1,79$ $p < .029$).

Cell 5: Figure 9 shows both strains spent more time in Cell 5 in the predator condition than in the no predator condition but the difference between conditions was greater for Wistars than for Hoodeds, with Wistars having a higher level in the predator condition. This F result did not contribute to the multivariate discrimination, however[1] ($F = 4.124$ $df = 1,79$ $p < .046$).

AD: STRAIN x DRUG

The two way interaction of strain x drug resulted in a significant multivariate F test ($F = 2.078$ DF HYP = 14.00

1. Throughout all the main effects and interactions, the criterion Cell 5 did not contribute to the multivariate significance. Results concerning Cell 5 should thus be interpreted with caution.

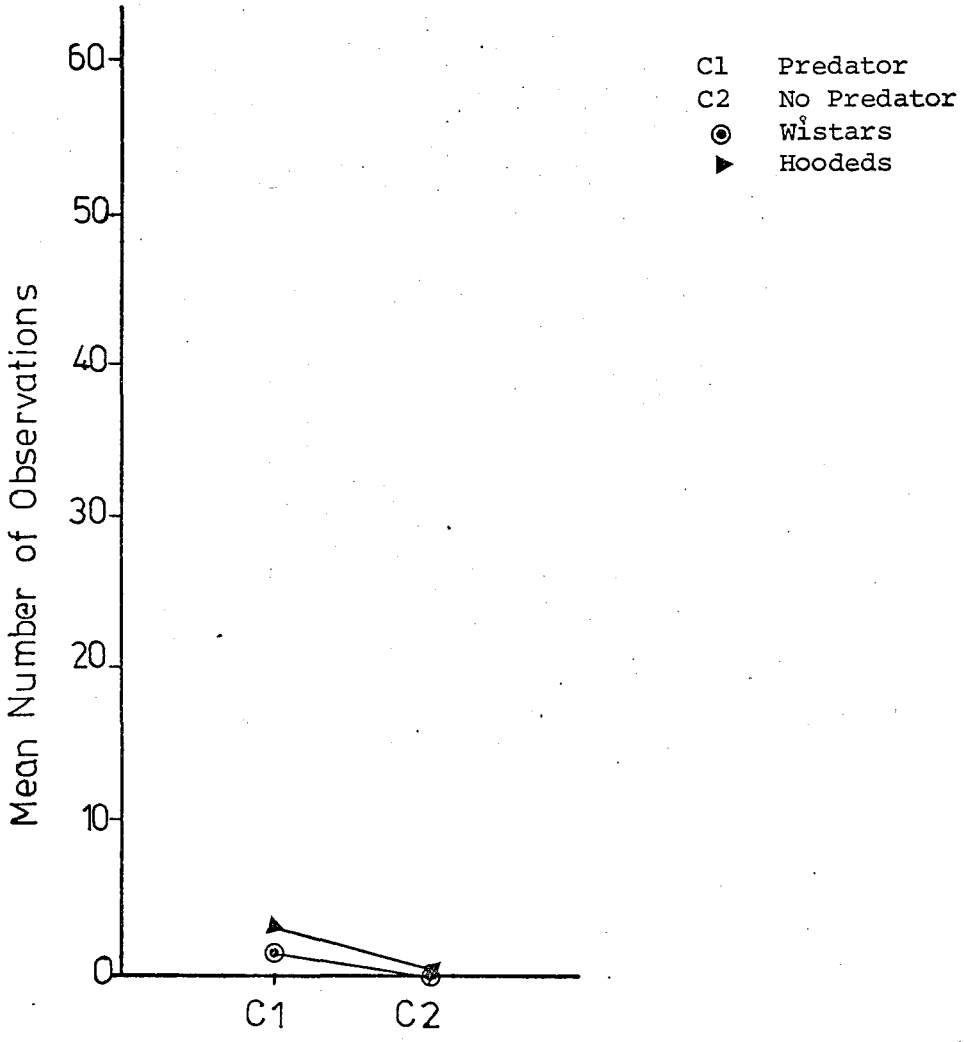

Figure 8 Approach-Avoidance Scores for the Strain x Predator Interaction

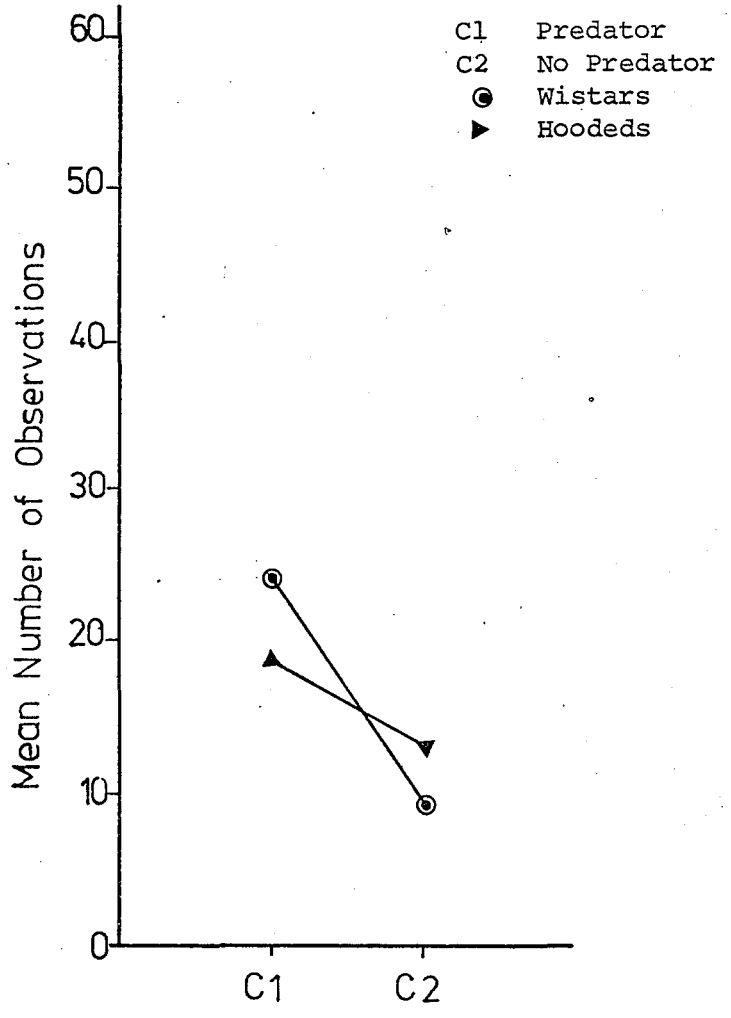

Figure 9 Cell 5 Scores for the Strain x Predator Interaction.

DF ERR = 66.00 $p < .024$ R = 0.553). The standardised discriminant function equation for the interaction was as follows:

$$V_{AD} = -5.476(IMM) - 4.113(LOCO) - 4.026(REAR) - 3.943(SNIF) - 1.954(GROO) + 0.987(CELL\ 1) - 0.629(LAT) + 0.597(CELL\ 2) + 0.426(LXX) + 0.354(CELL\ 4) - 0.334\ (A\text{-}A) + 0.314(CELL\ 3) + 0.157(FREEZ) + 0.00(CELL\ 5),$$

from which it can be seen that Immobility, Locomotion, Rearing, Sniffing and Grooming contributed most to the multivariate discrimination. On the discriminant dimension used in the significant multivariate F test, the contrasts are represented as deviations (-0.605 and 0.605) from the AD interaction grand mean ($\overline{AD}$) which is set at zero.

One criterion resulted in a significant univariate F test.

Locomotion: Figure 10 shows that Hoodeds locomoted more in the drug condition than in the no drug condition and that Wistars showed the opposite trend. Wistars overall showed more locomotion than Hoodeds, the largest difference being between strains on the drug control condition ($F = 9.922$ $df = 1,79$ $p < .002$).

BC: SEX x PREDATOR

The multivariate and univariate F tests on the two way interaction of sex x predator were not significant at the $p < .05$ level.

BD: SEX x DRUG

The multivariate F test of the two way interaction of sex x drug was not significant at the $p < .05$ level. Three

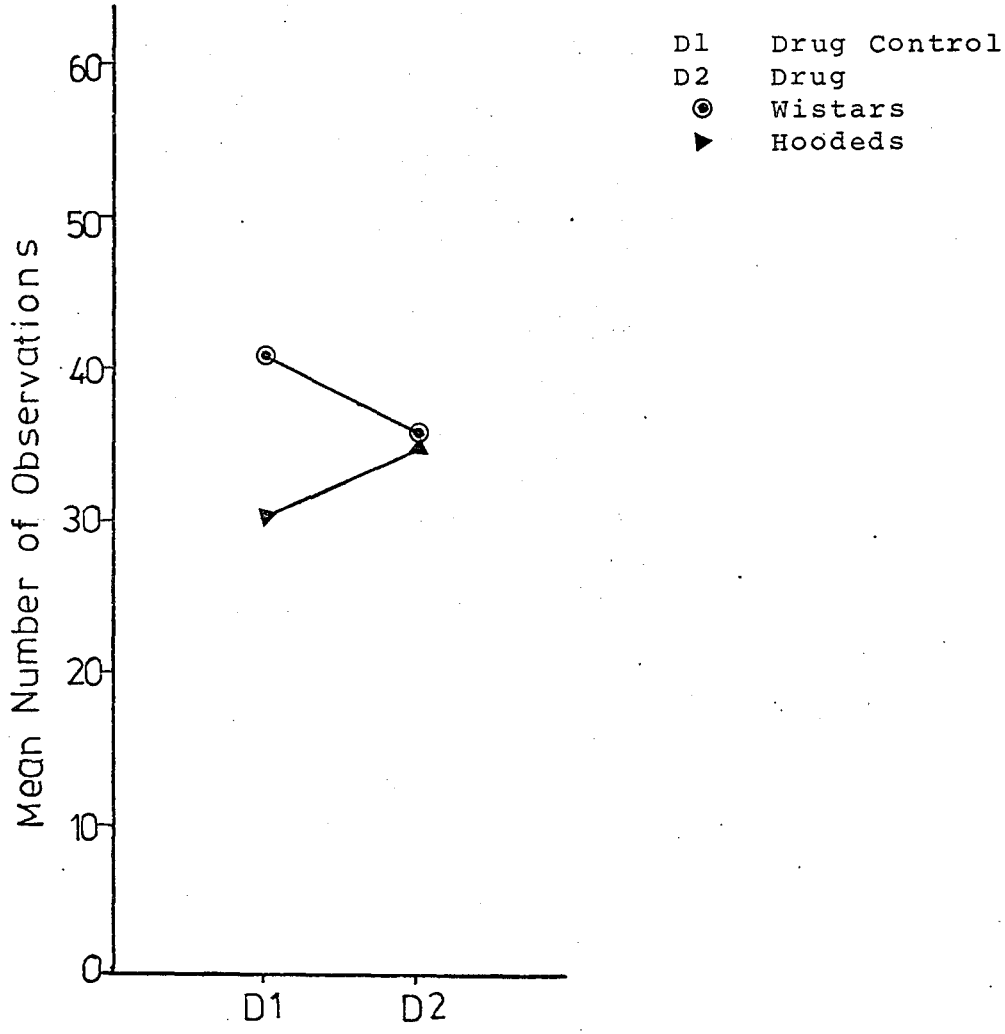

Figure 10 Locomotion Scores for the Strain x Drug Interaction.

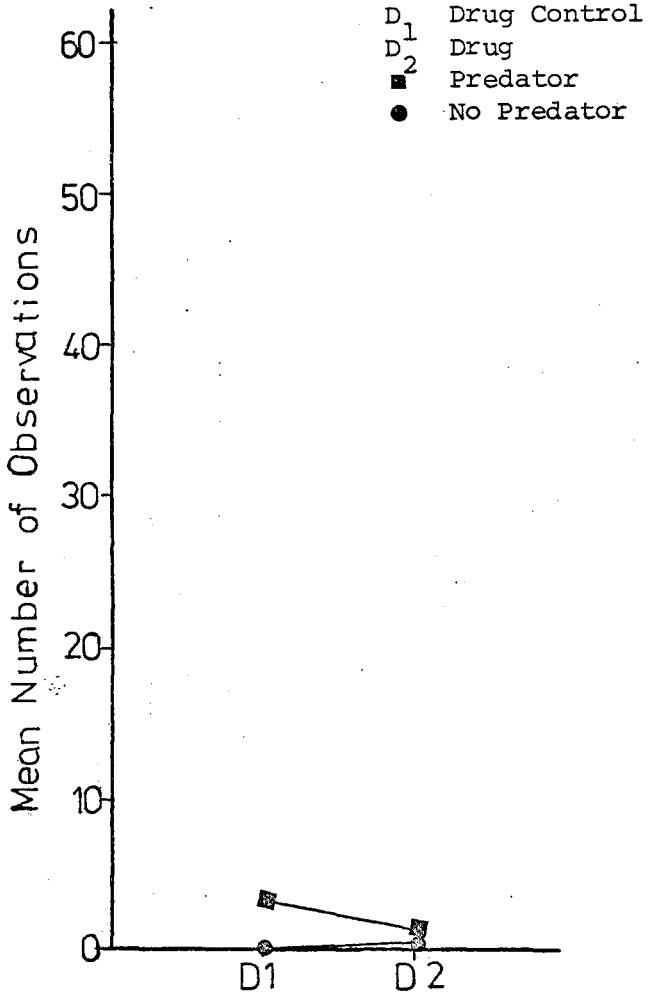

Figure 11 Approach-Avoidance Scores for the Predator x Drug Interaction

univariate F tests were significant: A-A ($F = 4.332$ df = 1,79 $p < .041$), CELL 2 ($F = 4.904$ df = 1,79 $p < .03$) and CELL 5 ($F = 12.759$ df = 1,79 $p < .001$).

CD: PREDATOR x DRUG

The two way interaction of predator x drug resulted in a significant multivariate F test ($F = 2.616$ DF HYP = 14.00 DF ERR = 66.00 $p < .005$ $R = 0.597$). The standardised discriminant function equation for this interaction was as follows:

$$V_{CD} = -5.737(IMM) - 4.455(REAR) - 4.28(SNIF) - 3.846(LOCO) - 2.099(GROO) + 1.405(CELL\ 1) - 1.187(A\text{-}A) + 1.098(CELL\ 2) + 0.721(CELL\ 4) - 0.599(LAT) + 0.440(LXX) + 0.307(FREEZ) + 0.208(CELL\ 3) + 0.00(CELL\ 5),$$

from which it can be seen that Immobility, Rearing, Sniffing, Locomotion and Grooming contributed most to the multivariate discrimination. On the discriminant dimension used in the significant multivariate F test, the contrasts are represented as deviations (-0.673 and 0.673) from the CD interaction grand mean ($\overline{CD}$) which is set at zero.

Univariate F tests were significant on two criteria.

Approach-Avoidance: Figure 11 shows there was a large difference between animals in the predator group and those in the no predator group; predator animals engaged in more approach-avoidance than no predator animals and this was more marked in the drug control as opposed to the drug condition. Animals in the no predator condition had larger values of approach-avoidance if they were also drugged rather than those

in the drug control condition, but the reverse was true of those in the predator condition ($F = 8.590$ df = 1,79 $p < .004$).

Cell 5: Figure 12 shows that animals in both the predator and no predator conditions had similar trends when the drug conditions are compared; animals in the drug condition spent less time in Cell 5 than those in the drug control condition. However, animals in the predator condition spent more time in Cell 5 than the no predator controls, this difference being more marked in the drug control condition ($F = 4.107$ df = 1,79 $p < .046$).

ABC: STRAIN x SEX x PREDATOR

The multivariate F test of the three way interaction of strain x sex x predator was significant ($F = 2.104$ DF HYP = 14.00 DF ERR = 66.00 $p < .023$ $R = 0.556$).

The standardised discriminant function equation for this interaction was as follows:

$$V_{ABC} = -9.277(IMM) - 6.020(REAR) - 5.075(SNIF) - 4.791(LOCO) - 4.050(GROO) - 0.909(A\text{-}A) - 0.897(CELL\ 1) - 0.796(LXX) - 0.520(CELL\ 2) + 0.480(LAT) - 0.409(FREEZ) - 0.349(CELL\ 4) \quad 0.217(CELL\ 3) + 0.00(CELL\ 5),$$

from which it is apparent that Immobility, Rearing, Sniffing, Locomotion and Grooming contributed most to the multivariate significance. On the discriminant dimension used in the significant multivariate F test, the contrasts are represented as deviations (-0.603 and 0.603) from the ABC interaction grand mean ($\overline{ABC}$) which is set at zero.

There were four significant univariate F tests.

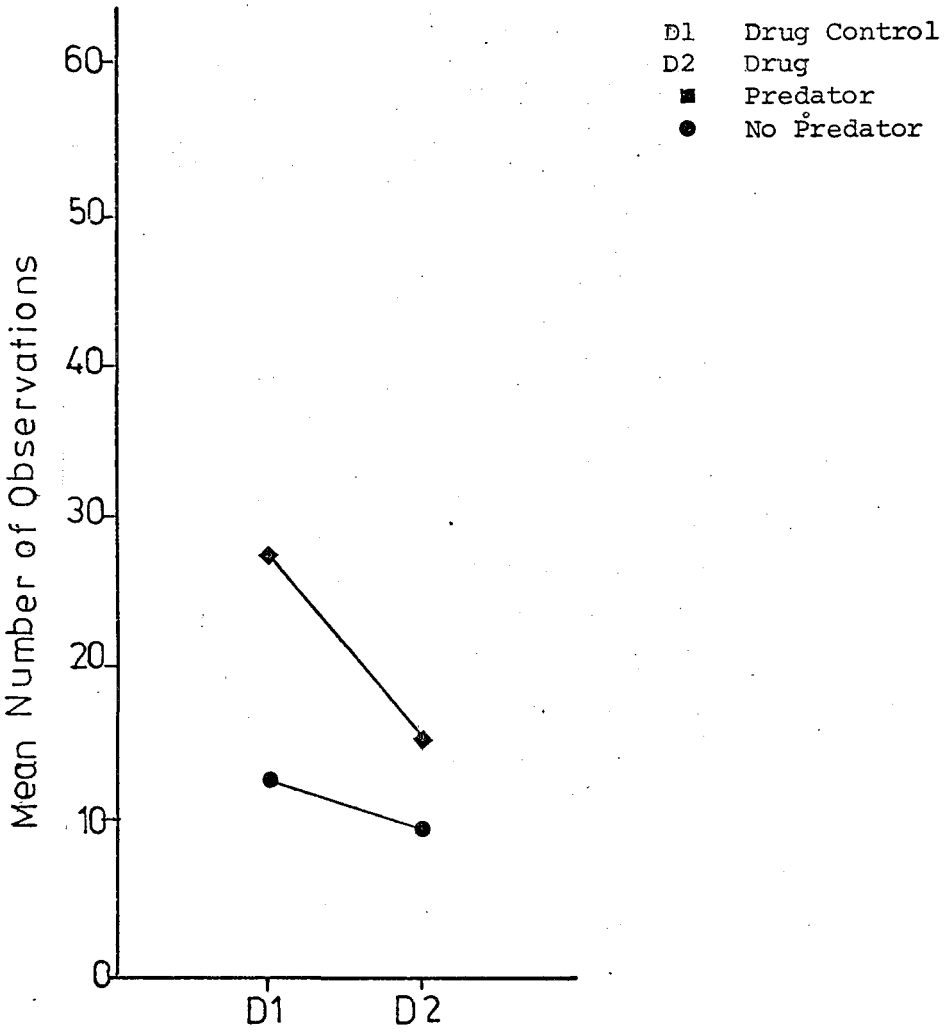

Figure 12 Cell 5 Scores for the Predator x Drug Interaction

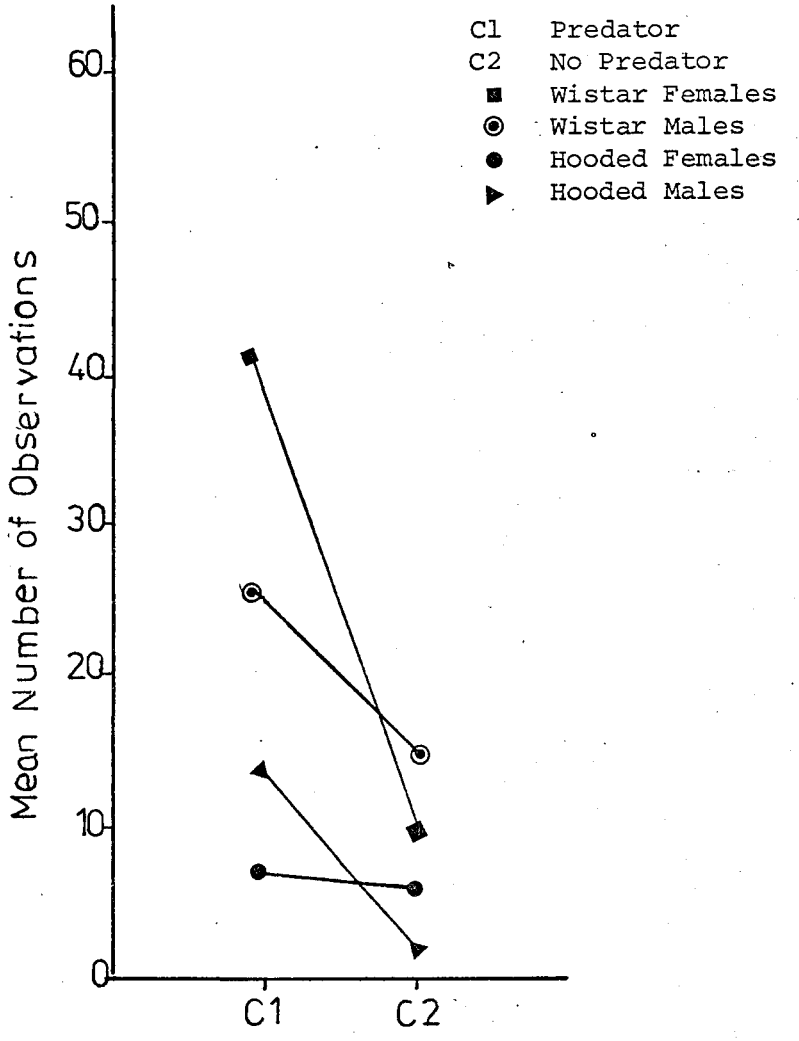

Figure 13 Immobility Scores for the Strain x Sex x Predator Interaction.

Immobility: Figure 13 shows that for both strains and sexes, animals in the no predator condition were less immobile than those in the predator condition. However, Wistars had greater immobility than Hoodeds with Wistar females demonstrating the largest amount of immobility in the predator condition and the largest drop in the no predator condition. Hooded females showed little difference between the predator conditions. The slope of the data for Wistar males was similar to that for Hooded males except the Wistars were higher in absolute level ($F = 7.843$ $df = 1,79$ $p < .006$).

Rearing: Figure 14 demonstrates that for both strains and sexes, animals in the no predator condition reared more than those in the predator condition. Hooded rats of both sexes had higher levels than Wistars in the predator condition, while Hoodeds and Wistar females reared more than Wistar males in the no predator condition. Wistar females showed the largest difference between presence or absence of a predator ($F = 6.433$ $df = 1,79$ $p < .013$).

Grooming: Figure 15 is a difficult interaction to interpret due to the large differences between all four groups of animals. However, Hooded males and Wistar females showed a similar amount of grooming in the no predator condition and both increased grooming in the predator condition. This increase was greater for Hooded males.

Both Wistar males and Hooded females decreased grooming in the predator condition although Hooded females had a much greater difference. Reactivity was greater for Hoodeds of both sexes even though the trend differs between the predator conditions.

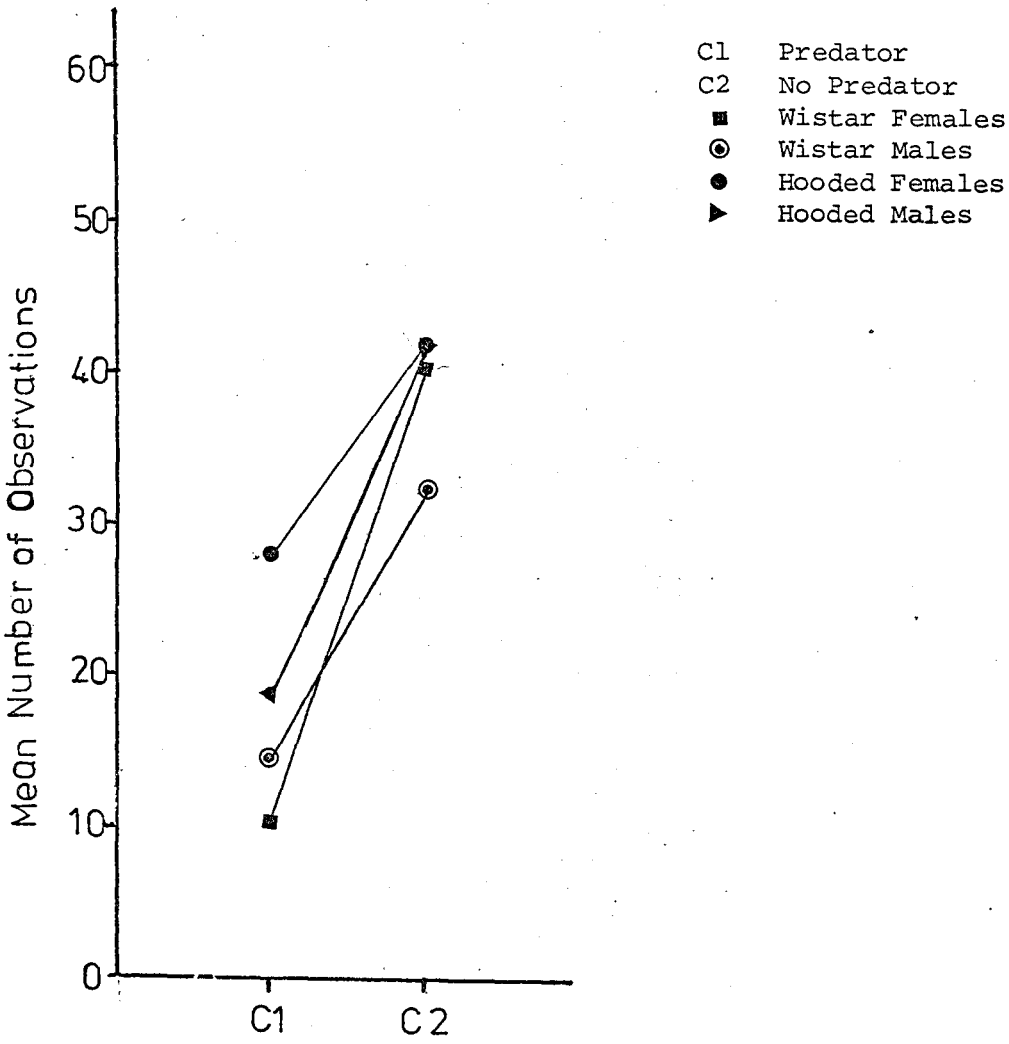

Figure 14 Rearing Scores for the Strain x Sex x Predator Interaction

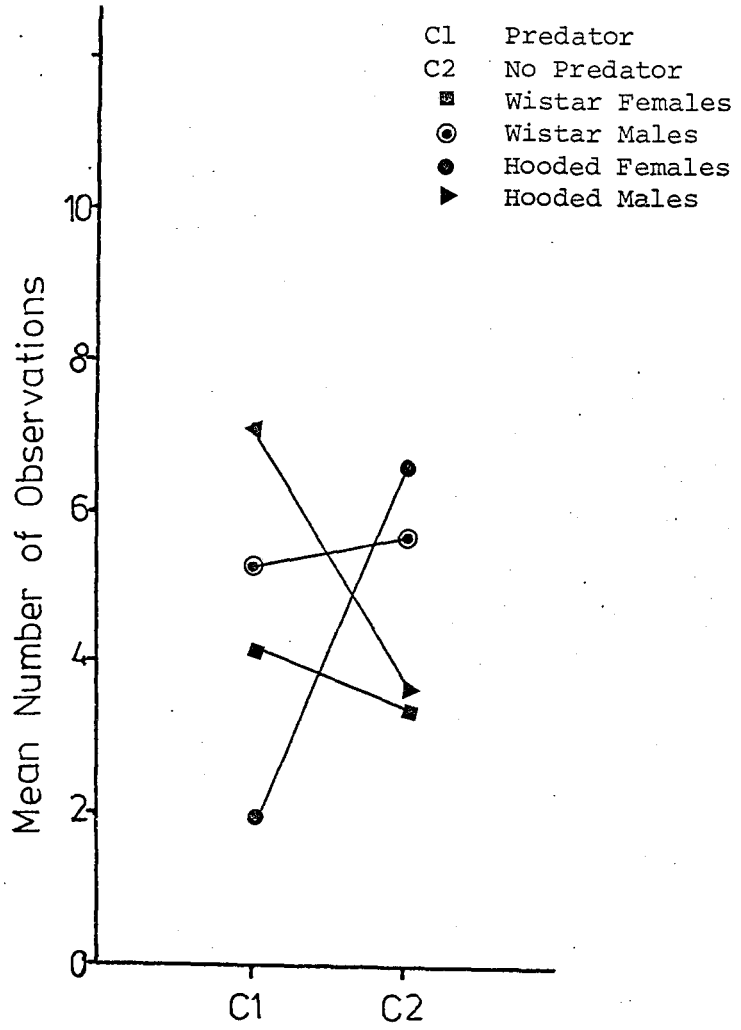

Figure 15 Grooming Scores for the Strain x Sex x Predator Interaction.

Males of both strains groomed more in the predator condition than females while in the no predator condition this grouping disappeared ($F = 4.242$ df = 1,79 $p < .043$).

Cell 3: Figure 16 shows that both strains and sexes spent less time in Cell 3 if in the no predator condition than in the predator condition. For Hooded males and Wistar females this difference was not great, but for Wistar males and Hooded females the increased time in Cell 3 when the predator was present, was more marked ($F = 4.468$ df = 1,79 $p < .038$).

ABD: STRAIN x SEX x DRUG

The three way interaction of strain x sex x drug resulted in a significant multivariate F test ($F = 2.833$ DF HYP = 14.00 DF ERR = 66.00 $p < .002$ $R = 0.613$). The standardised discriminant function equation for this interaction was:

$$V_{ABD} = 3.154(IMM) + 2.928(REAR) + 1.724(SNIF) + 1.465(GROO) + 1.367(CELL\ 1) + 1.214(LOCO) + 1.067(CELL\ 2) + 1.01(CELL\ 4) + 0.546(FREEZ) + 0.445(A\text{-}A) - 0.20(CELL\ 3) - 0.105(LXX) - 0.071(LAT) + 0.00(CELL\ 5),$$

from which it appears that Immobility, Rearing, Sniffing, Grooming, Cell 1, and Locomotion contributed most to the multivariate discrimination. On the discriminant dimension used in the significant multivariate F test, the contrasts are represented as deviations (0.709 and -0.709) from the ABD interaction grand mean ($\overline{ABD}$) which is set at zero.

Univariate F tests yielded four significant results.

Rearing: Figure 17 shows that Wistar males and Hooded females had similar sloped lines with both groups rearing more

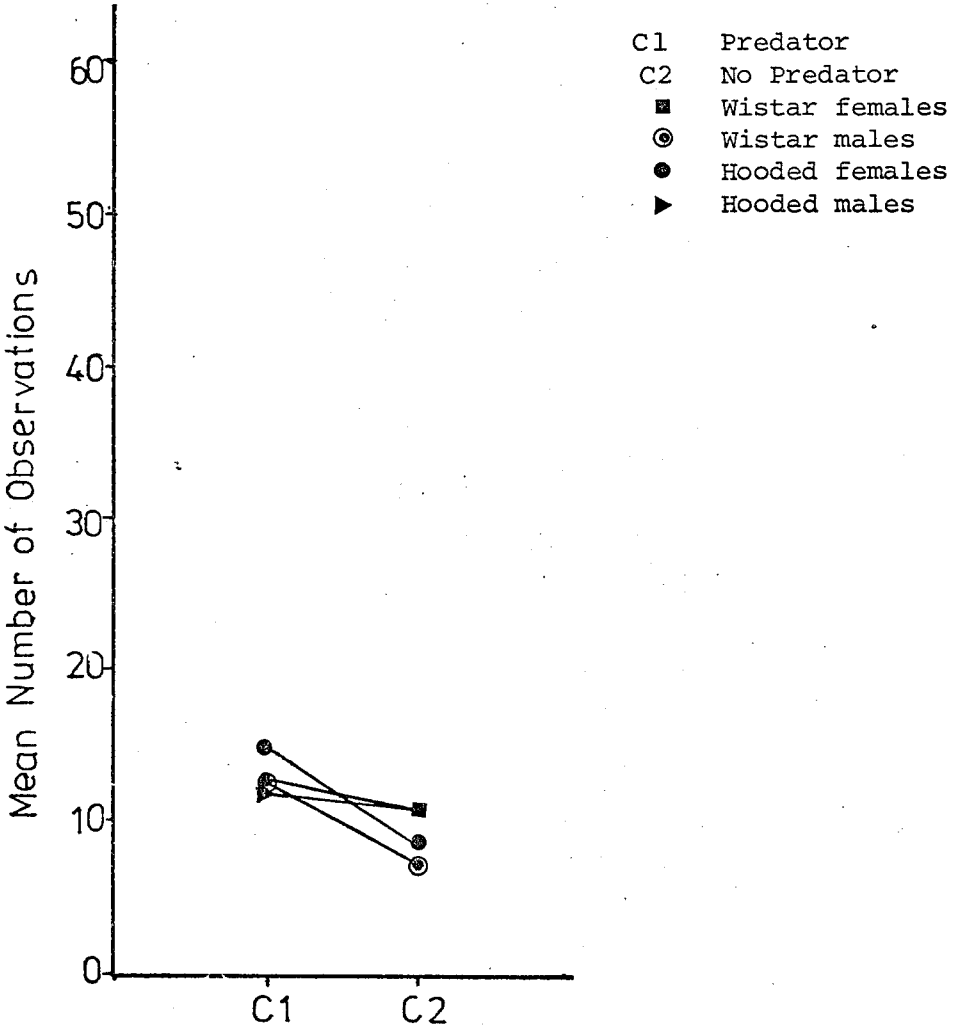

Figure 16 Cell 3 scores for the Strain x Sex x Predator Interaction

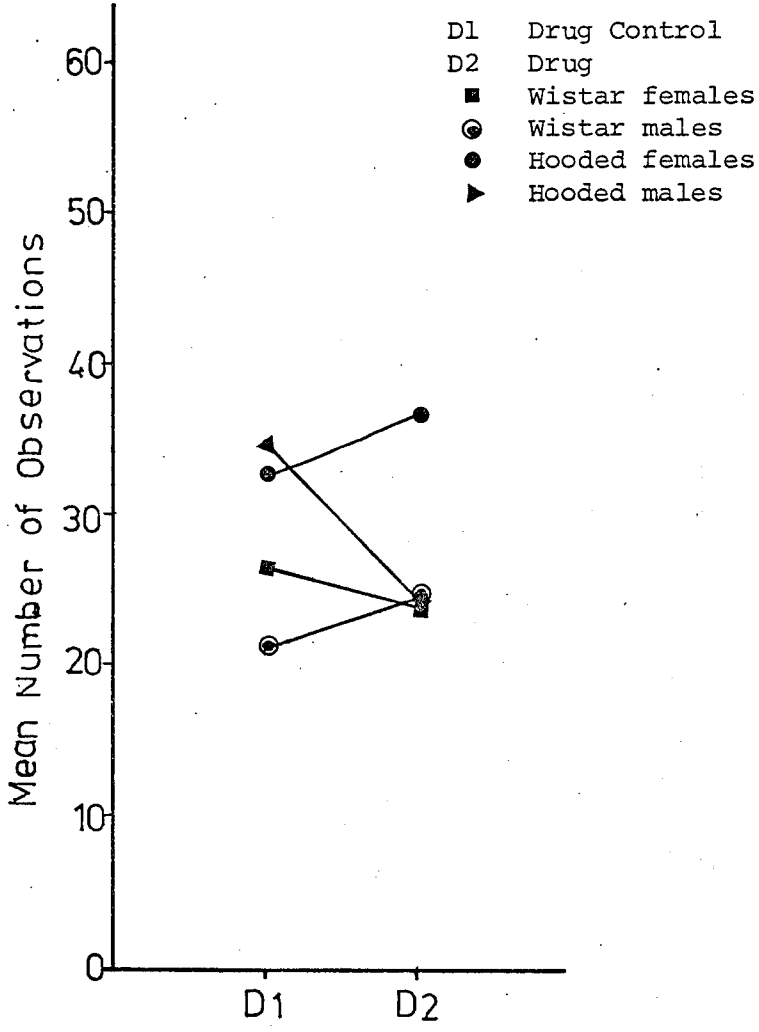

Figure 17 Rearing Scores for the Strain x Sex x Drug Interaction.

in the drug condition than in the control, although the Hooded females had a higher absolute level. Hooded males and Wistar females showed the opposite results and Hooded males had a higher level of rearing in the drug control condition than Wistar females. Three groups were close in level in the drug condition: Wistar males and females, and Hooded males whereas in the drug control condition the sexes of each strain were similar in level with Hoodeds being higher than Wistars ($F = 6.079$ $df = 1,79$ $p < .016$).

Locomotion: Figure 18 shows that both strains of females had similar levels of locomotion regardless of drug condition, but Wistar females had a higher absolute level in both conditions. Hooded males had a higher level of locomotion in the drug condition than in drug control, while Wistar males showed the opposite results. The trend of the data for all groups except Wistar males was for drugged animals locomoting more than undrugged ones. Undrugged Wistars locomoted more than undrugged Hoodeds, regardless of sex. However, drugged animals did not show this grouping. Instead, the Hooded males and Wistar females locomoted more than the Wistar males and Hooded females. ($F = 8.984$ $df = 1,79$ $p < .004$).

Cell 1: Figure 19 indicates that Hoodeds of both sexes and Wistar males spent more time in Cell 1 if drugged than those undrugged, whereas Wistar females spent less time in Cell 1 if also drugged. Hoodeds of both sexes and Wistar males were at a similar level if they were undrugged and this was lower than undrugged Wistar females. But, if drugged, the Wistar females had the same level as Hooded males while Hooded females and Wistar males were at much higher levels. ($F = 4.360$ $df = 1,79$ $p < .040$).

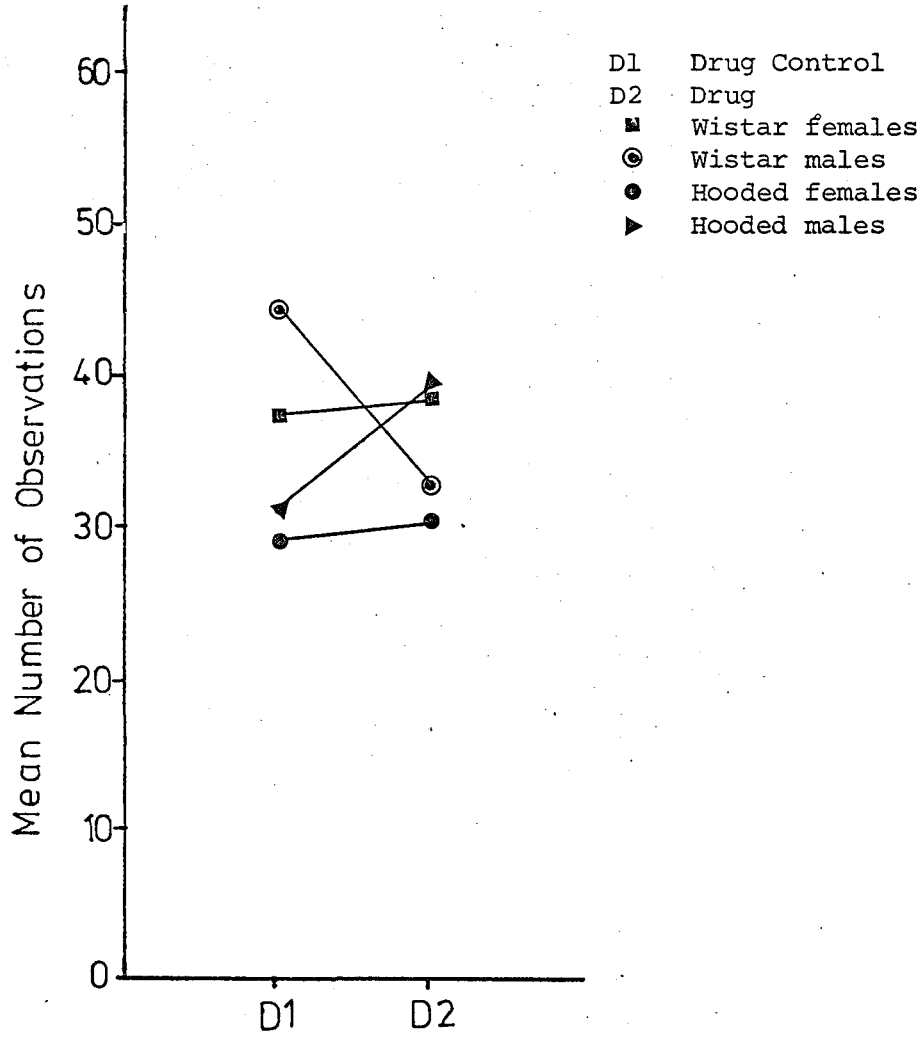

Figure 18 Locomotion Scores for the Strain x Sex x Drug Interaction

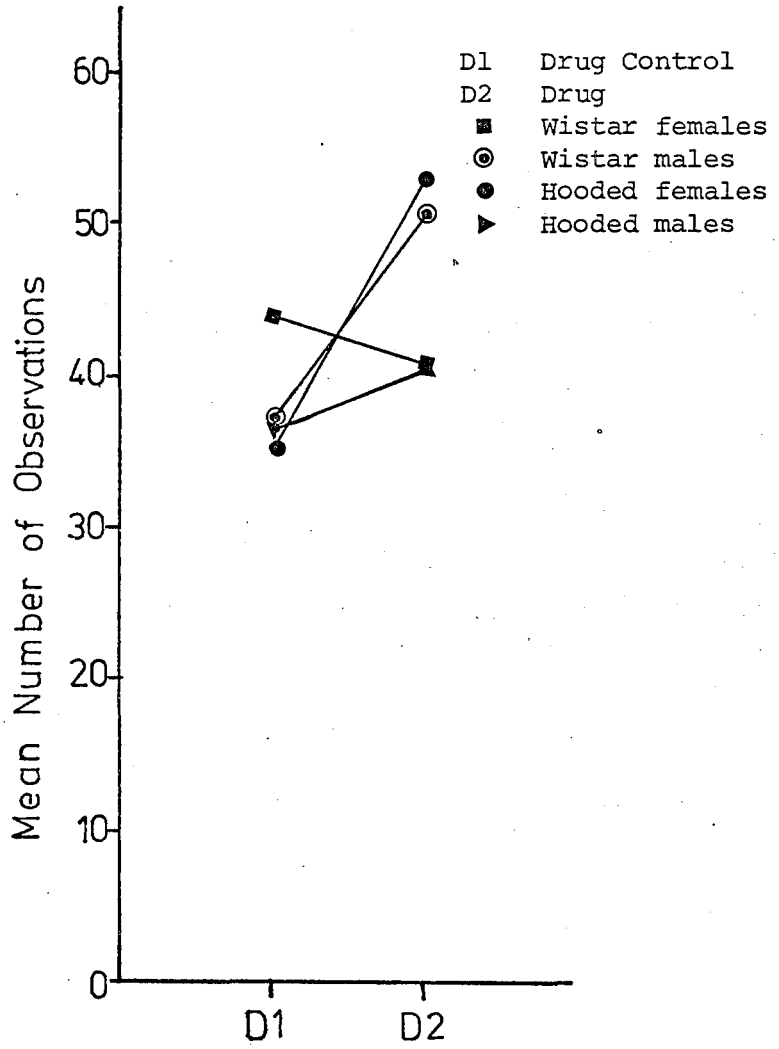

Figure 19 Cell 1 Scores for the Strain x Sex x Drug Interaction

Cell 5: Figure 20-Hoodeds of both sexes and Wistar males spent less time in Cell 5 in the drug condition compared with the controls, while Wistar females show the opposite results. Wistar males had the most marked difference between conditions, the other three groups being close together in both conditions although the slopes of their lines varied ($F = 5.715$ df = 1,79 $p < .019$).

ACD: STRAIN x PREDATOR x DRUG

The three way interaction of strain x predator x drug was not significant at the $p < .05$ level for the multivariate F test. However, the univariate F tests revealed one significant F ratio: REAR ($F = 5.54$ df = 1,79 $p < .021$).

BCD: SEX x PREDATOR x DRUG

The three way interaction of sex x predator x drug resulted in a significant multivariate F test ($F = 2.015$ DR HYP = 14.00 DF ERR = 66.00 $p < .03$ $R = 0.547$). The standardised discriminant function equation was as follows:

$$V_{BCD} = 6.242(IMM) + 4.315(REAR) + 3.47(SNIF) + 3.166(LOCO) + 2.392(GROO) + 1.50(CELL\ 1) + 1.342(CELL\ 2) + 0.982(A\text{-}A) + 0.566(CELL\ 4) + 0.480(LXX) + 0.346(FREEZ) + 0.344(CELL\ 3) + 0.144(LAT) + 0.00(CELL\ 5),$$

from which it can be seen that Immobility, Rearing, Sniffing, Locomotion and Grooming contributed most to the multivariate discrimination. On the discriminant dimension used in the significant multivariate F test, the contrasts are represented as deviations (0.599 and -0.599) from the BCD interaction grand mean ($\overline{BCD}$) which is set at zero.

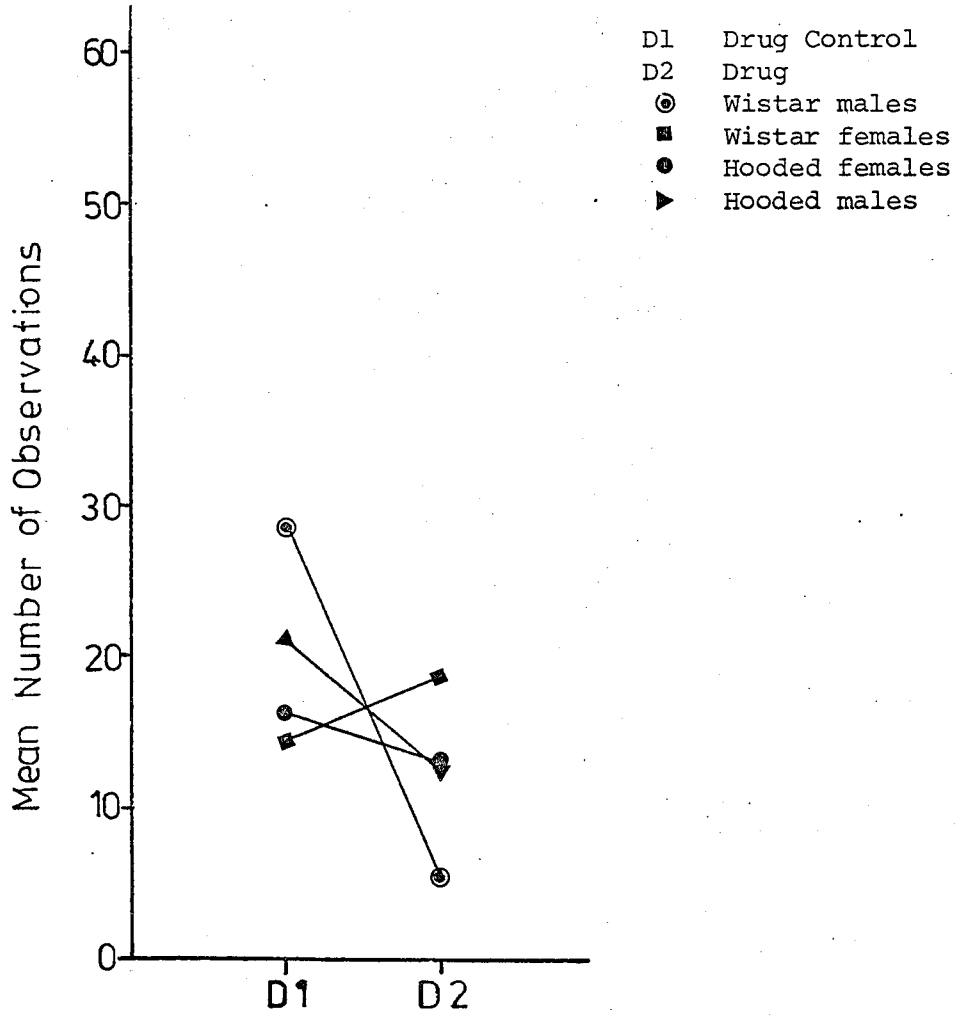

Figure 20 Cell 5 Scores for the Strain x Sex x Drug Interaction

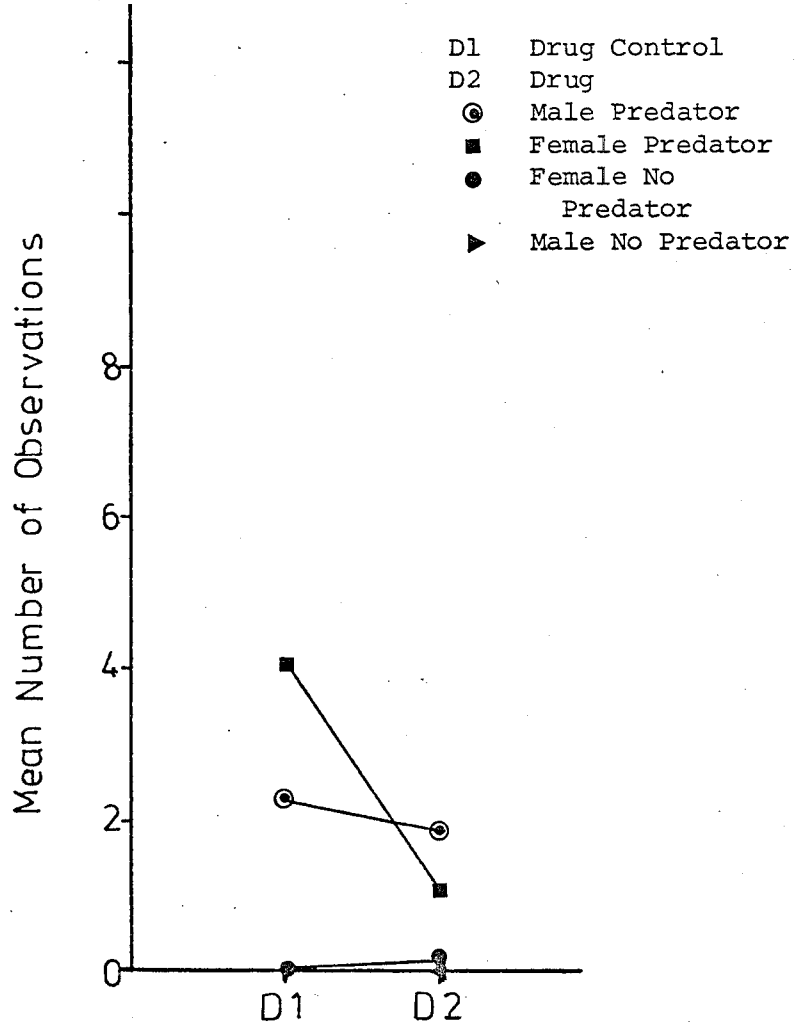

Figure 21 Approach-Avoidance Scores for the Sex x Predator x Drug Interaction

There were significant univariate F test results for three criteria.

Approach-Avoidance: Figure 21 shows that males in the predator condition had a higher absolute level of approach-avoidance than males in the no predator condition who remained at zero for both drug conditions. Males in the predator condition showed less approach-avoidance if drugged than if undrugged. In the drug condition, females increased approach-avoidance in the no predator condition over those in drug control. The opposite was true for females in the predator condition but drugged females of either predator condition were at a similar level. ($F = 5.03$ $df = 1,79$ $p < .028$).

Cell 2: Figure 22 - in the no predator condition, both sexes spent more time in Cell 2 if also drugged than those animals that were undrugged, with males having a slightly higher absolute level. In the predator condition, males were in Cell 2 more often if also drugged than undrugged and the reverse was true of females. Presence in Cell 2 was much higher for those in the predator condition as opposed to those in the no predator condition. ($F = 4.14$ $df = 1,79$ $p < .045$).

Cell 5: Figure 23 - Animals in the no predator condition spent less time in Cell 5 if also drugged rather than those undrugged animals, and the same trend was true for males in the predator condition except they had a higher level of presence in Cell 5 if undrugged. Females in the predator condition spent more time in Cell 5 when also drugged than those undrugged. ($F = 18.714$ $df = 1,79$ $p < .001$).

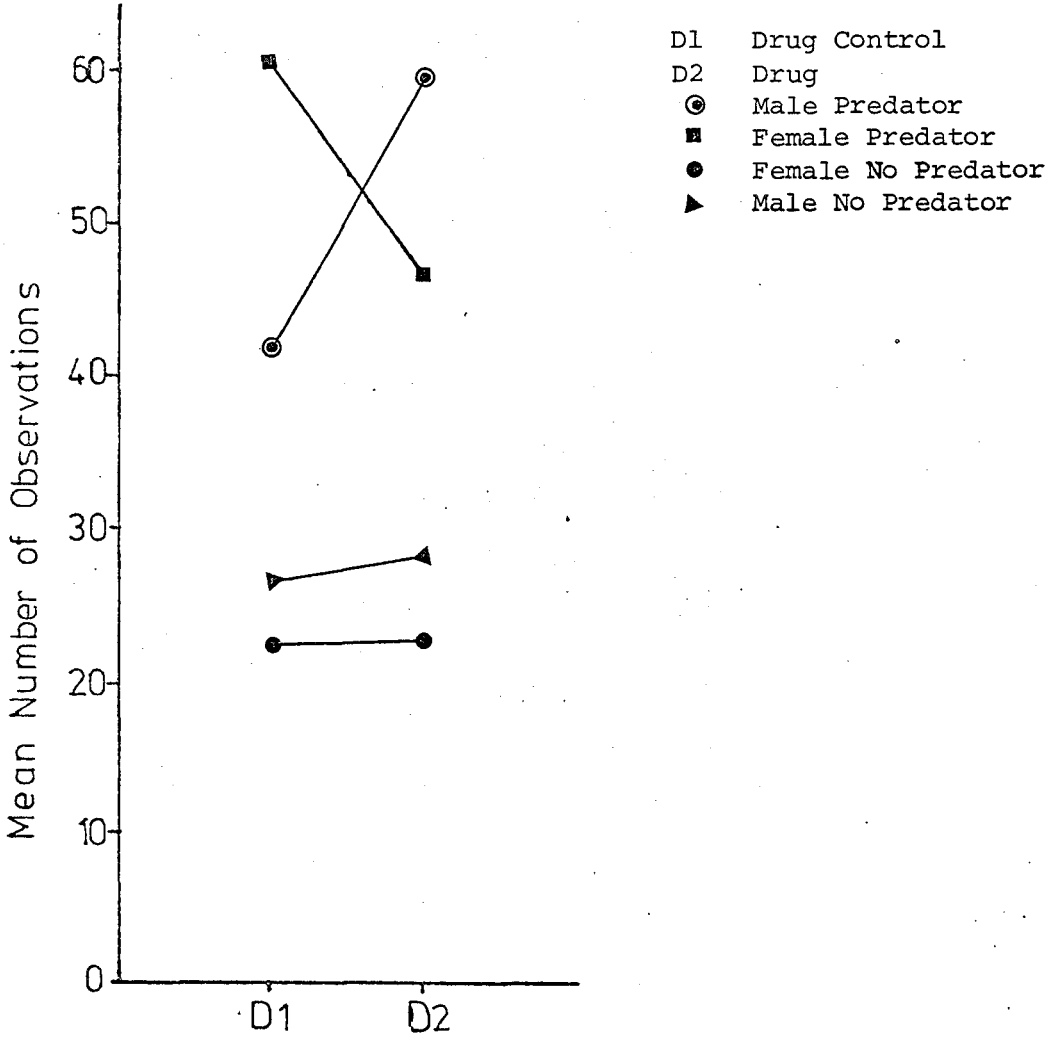

Figure 22 Cell 2 Scores for the Sex x Predator x Drug Interaction

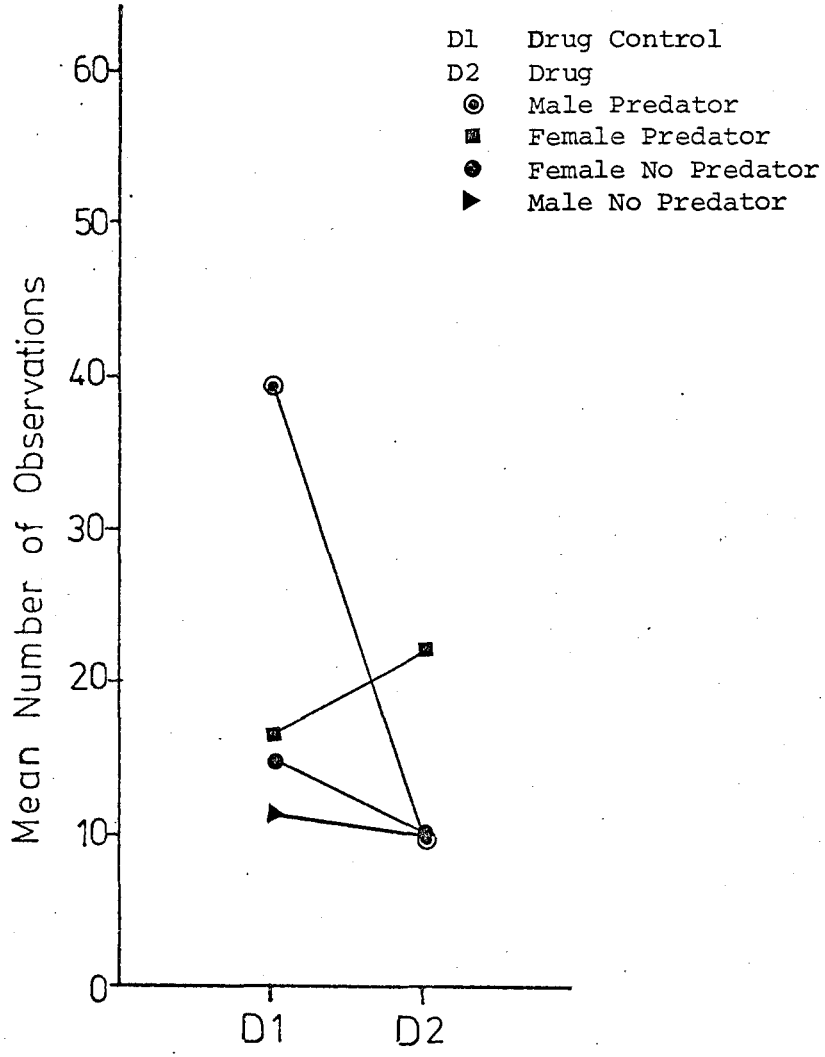

Figure 23 Cell 5 Scores for the Sex x Predator x Drug Interaction

ABCD: STRAIN x SEX x PREDATOR x DRUG

The four way interaction of strain x sex x predator x drug resulted in a significant multivariate F test ($F = 2.35$ DF HYP = 14.00 DF ERR = 66.00 $p < .01$ $R = 0.577$).

Univariate F tests on each of the dependent variables were not significant however, suggesting that the multivariate significance was a statistical artifact, possibly due to the small number of observations (6) in each group at this stage.

AN OVERVIEW

Figures 24, 25, 26 and 27 show presence in each segment of the runway for each level of the factors. These observations are expressed in percentages of the total number of observations. Both strains of animals spent similar amounts of time in each of the five parts of the runway, the only significant difference being that Hoodeds were more often in Cell 4 than Wistars. Presence in Cell 1 and Cell 2 was the most frequent and very little time was spent in Cells 3 and 4, but a moderate amount of time in Cell 5 occurred (Figure 24).

Both sexes also had very similar times in each part of the runway and there was no significant differences between the scores for each cell (Figure 25). The same pattern of preference in cells was evident as in the strain data.

The predator conditions were quite different in the distribution of presence in cells. As expected, little time was spent in close proximity to the predator (Cell 1), while control animals spent most of their time in this segment. Predator animals were seldom in Cells 3 and 4 but spent a moderate amount of time in Cells 2 and 5. No-predator controls

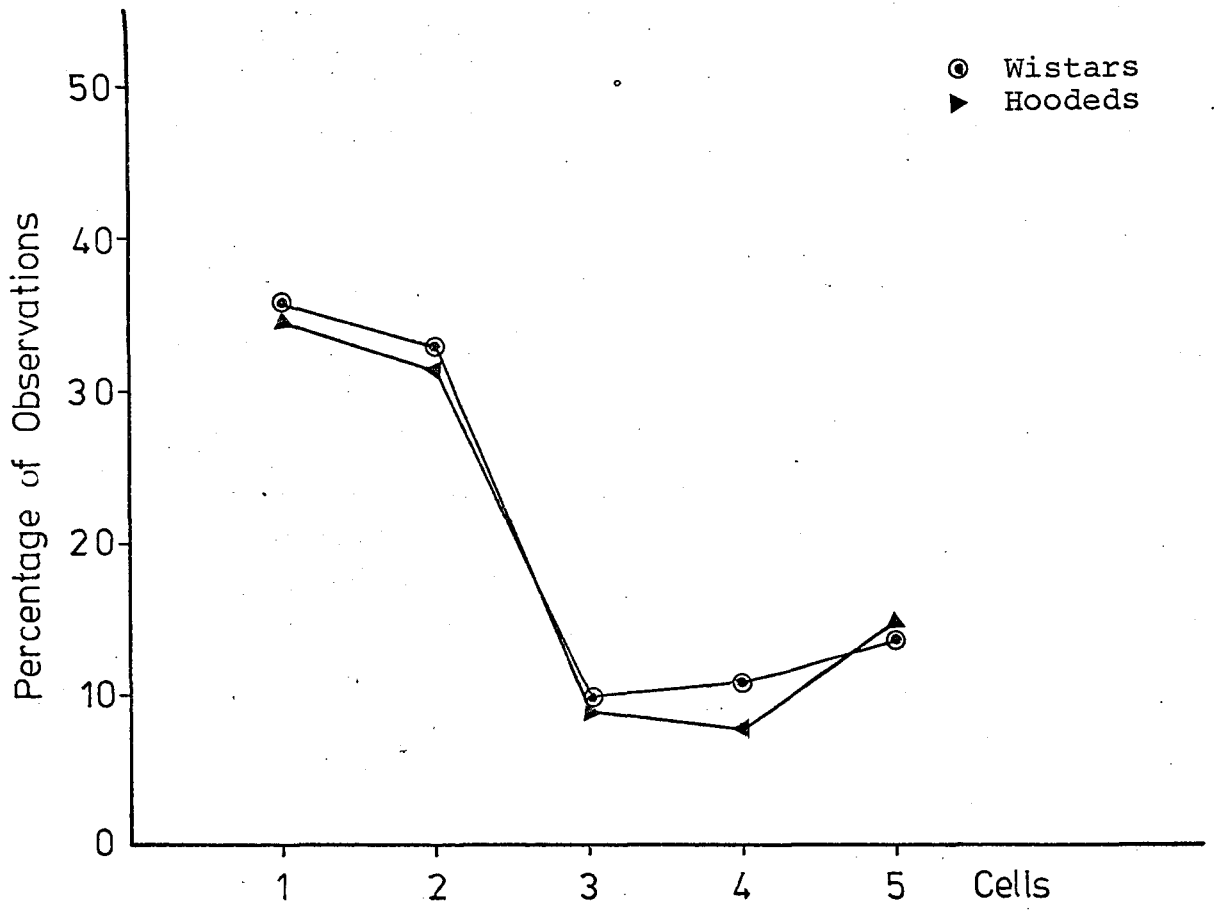

Figure 24 Presence in Each Cell of the Runway for the Strain Main Effect

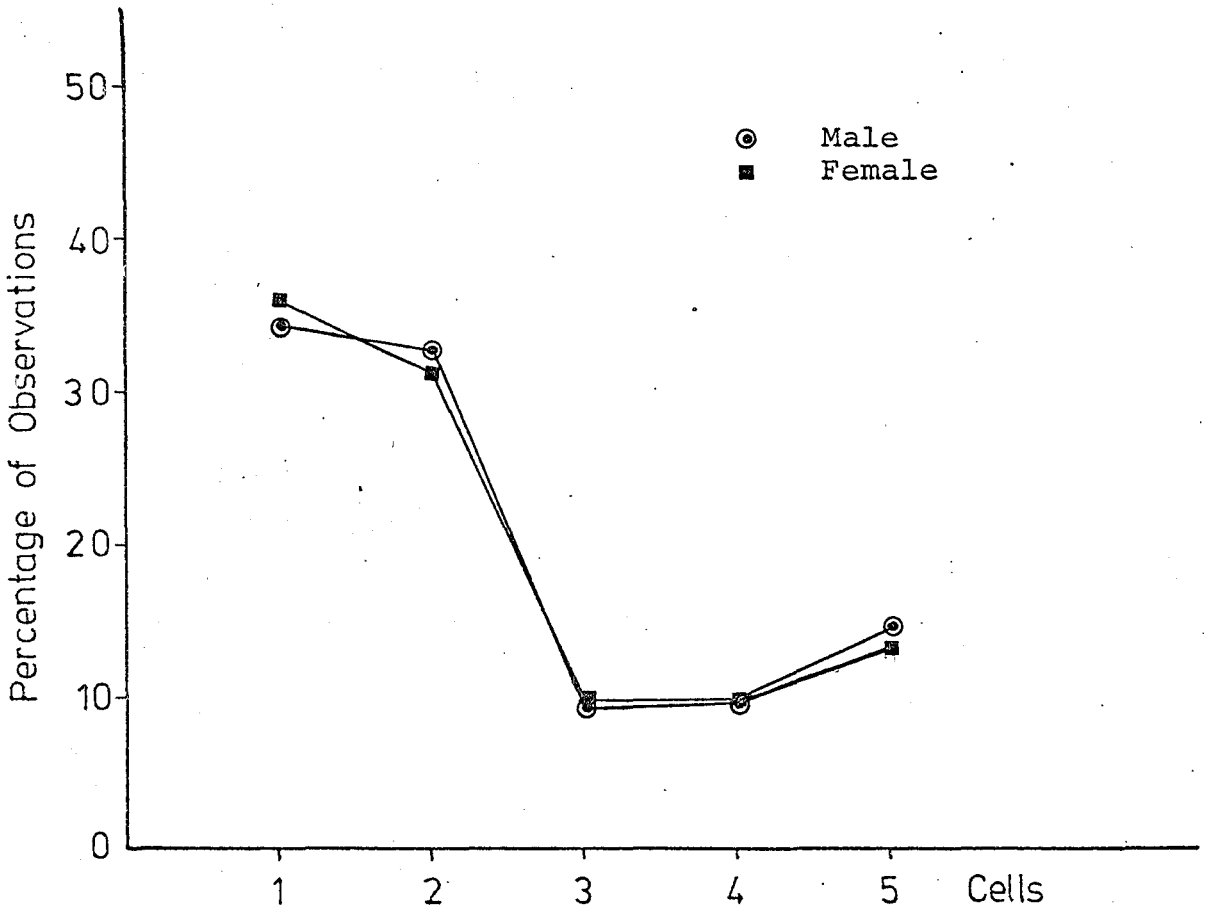

Figure 25 Presence in Each Cell of the Runway for the Sex Main Effect

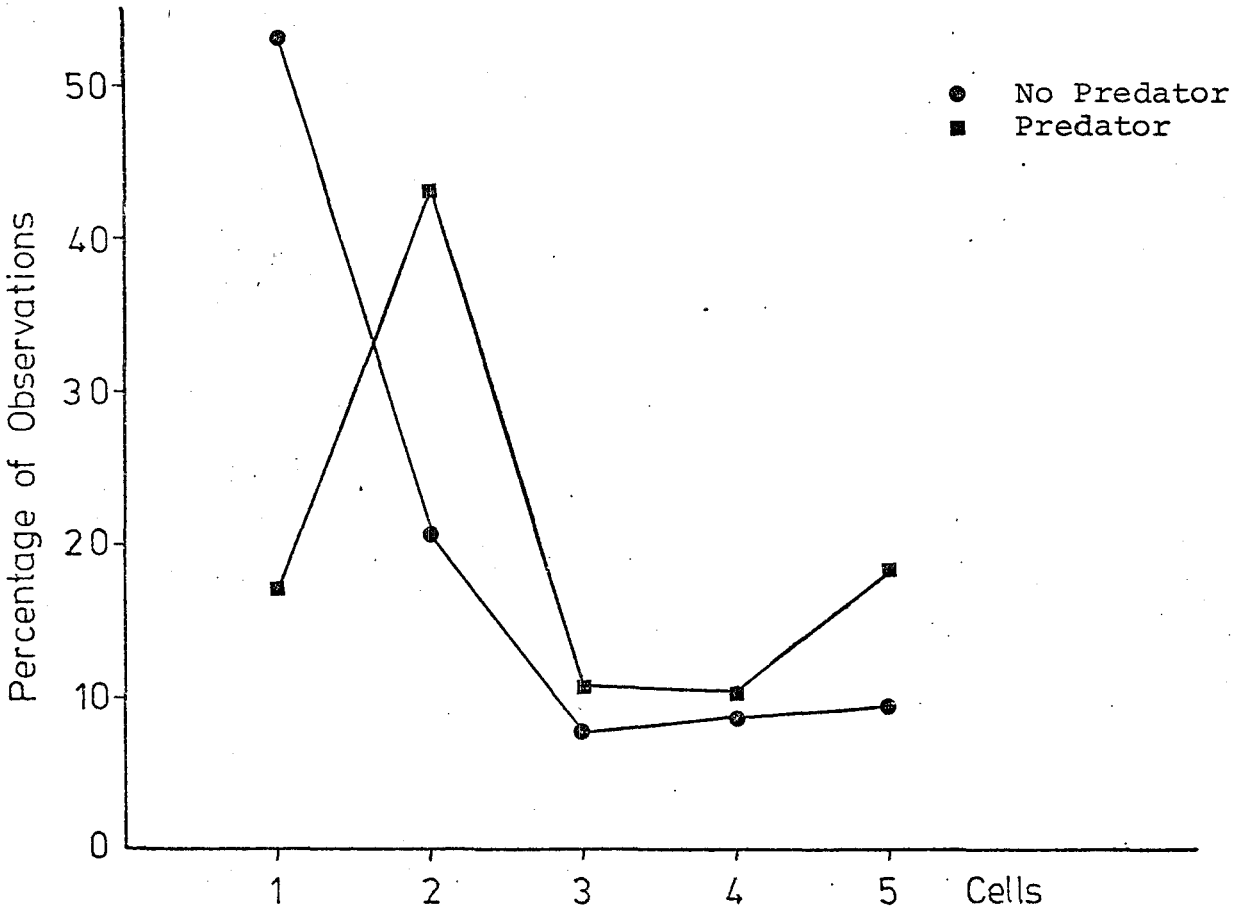

Figure 26 Presence in Each Cell of the Runway for the Predator Main Effect

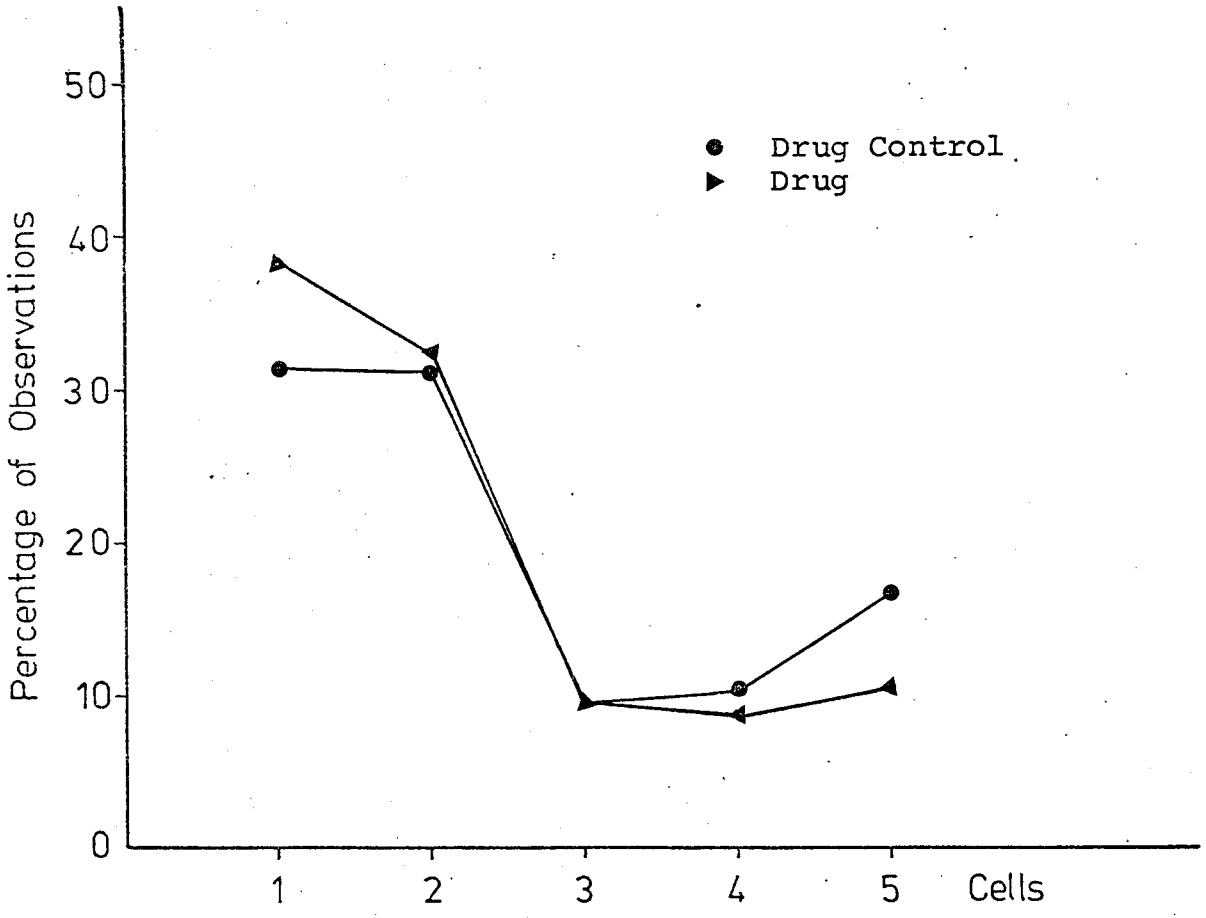

Figure 27 Presence in Each Cell of the Runway for the Drug Main Effect

spent little time in Cells 3, 4 and 5 and a moderate amount in Cell 2 (Figure 26).

Figure 27 shows that drug modification of presence in cells was mediated by drugged animals increasing time in Cell 1 and decreasing it in Cell 5. The pattern of time in cells was similar to the sex and strain data.

Likewise a similar analysis of the categories of general behaviour can be carried out. Figures 28, 29, 30, 31 demonstrate percentages of the total of observations of these categories. In general, rearing, locomotion, and sniffing were high frequency behaviours and freezing and approach-avoidance occurred rarely. Introduction of the predator caused increased immobility and decreased rearing. Wistars and drugged animals also had higher levels of immobility.

3.3 ANALYSIS TWO

In this analysis, trends over time were examined by considering each criterion in three parts; each part being equal to one third of the experimental time. Latency could not be divided in this manner, however.

This results in a new analysis with forty dependent variables. The table of within cells correlations (Table 7) is too lengthy to report here but can be found in Appendix 1. Inspection of the significant main effects and interactions indicate that there was no appreciable difference between each of the time periods, all three contributing to the significance in most cases. Very similar trends were observed over each time period.

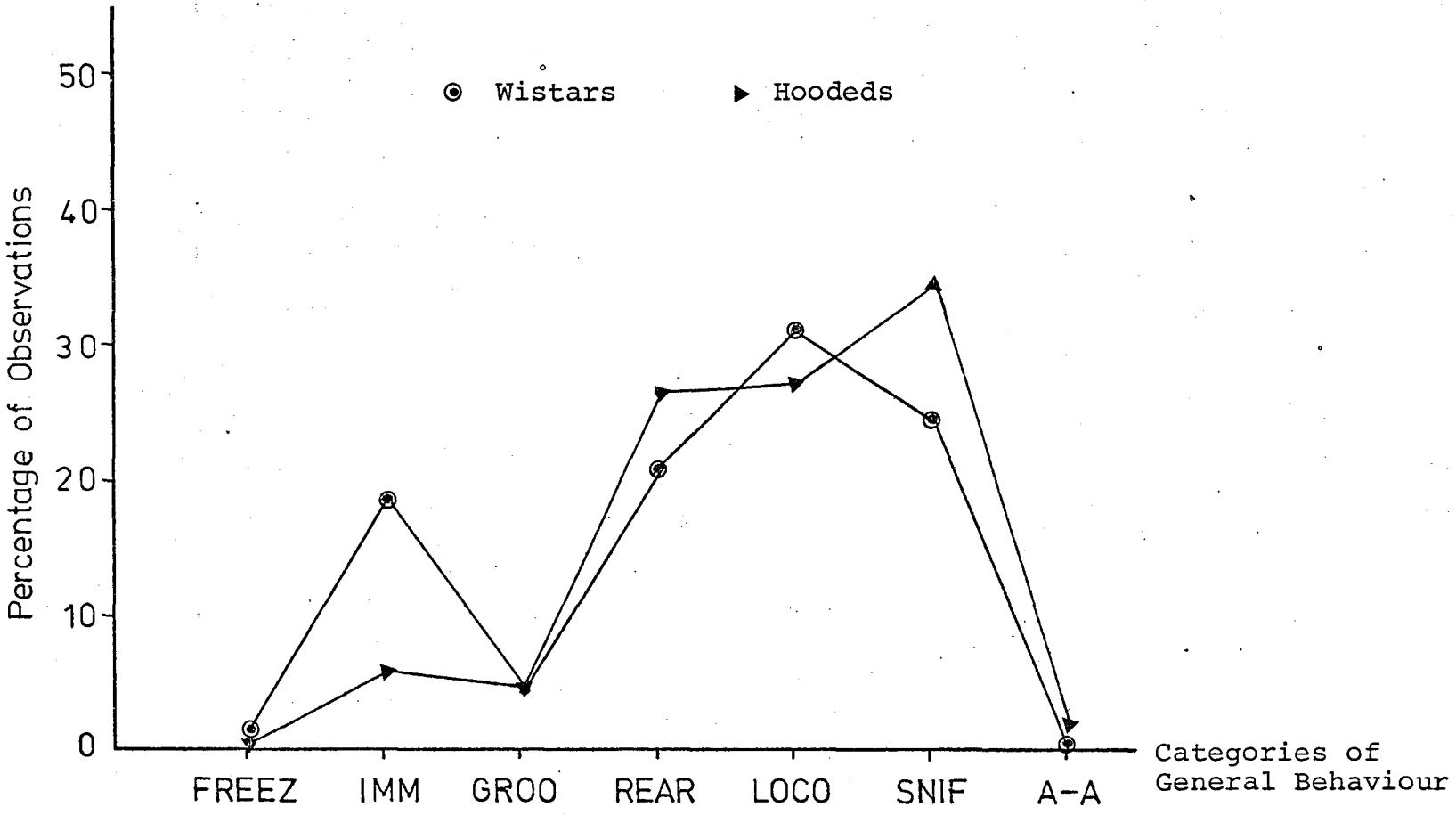

Figure 28 Percentage of Observations of Each Category of Behaviour for the Strain Main Effect

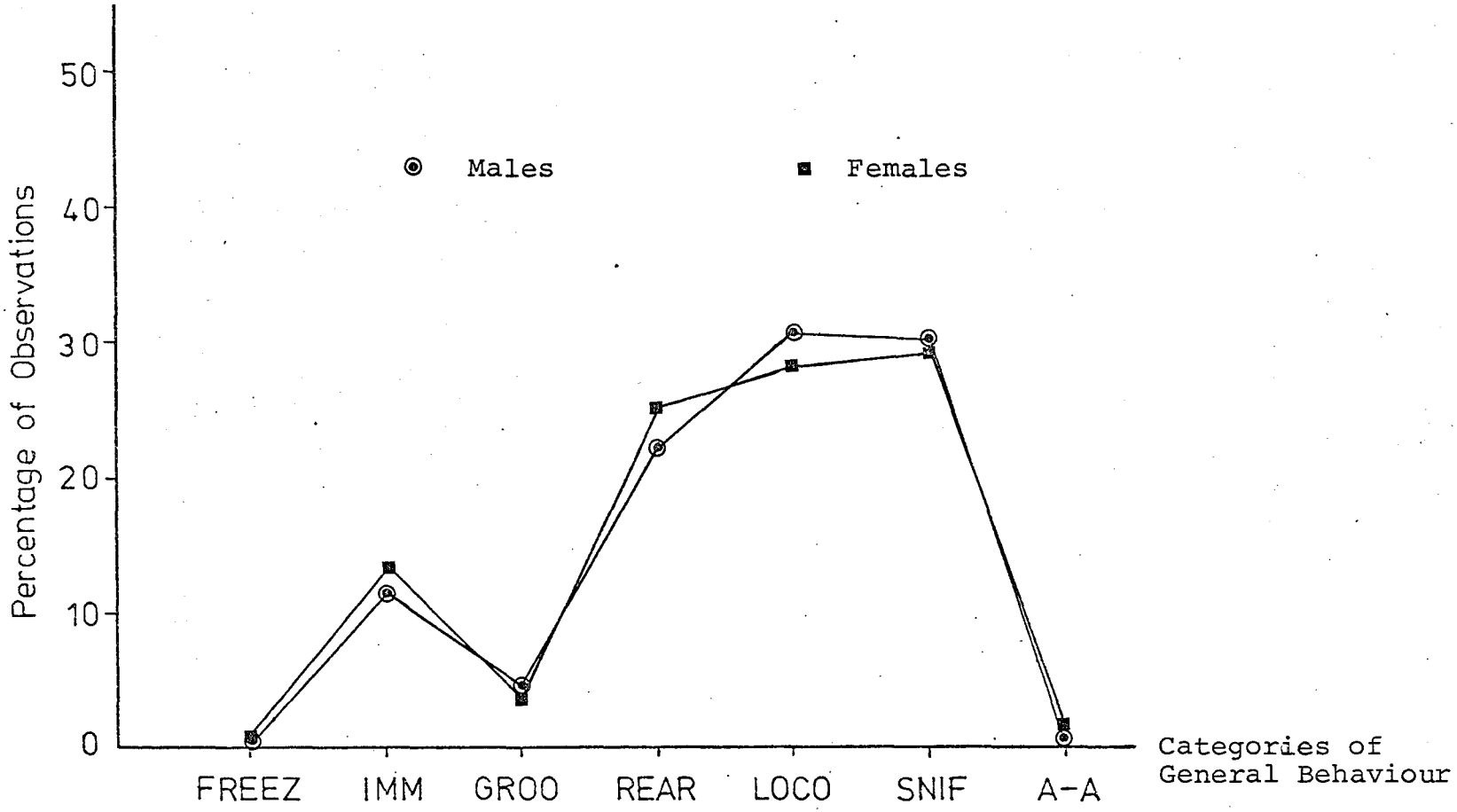

Figure 29 Percentage of Observations of Each Category of Behaviour for the Sex Main Effect

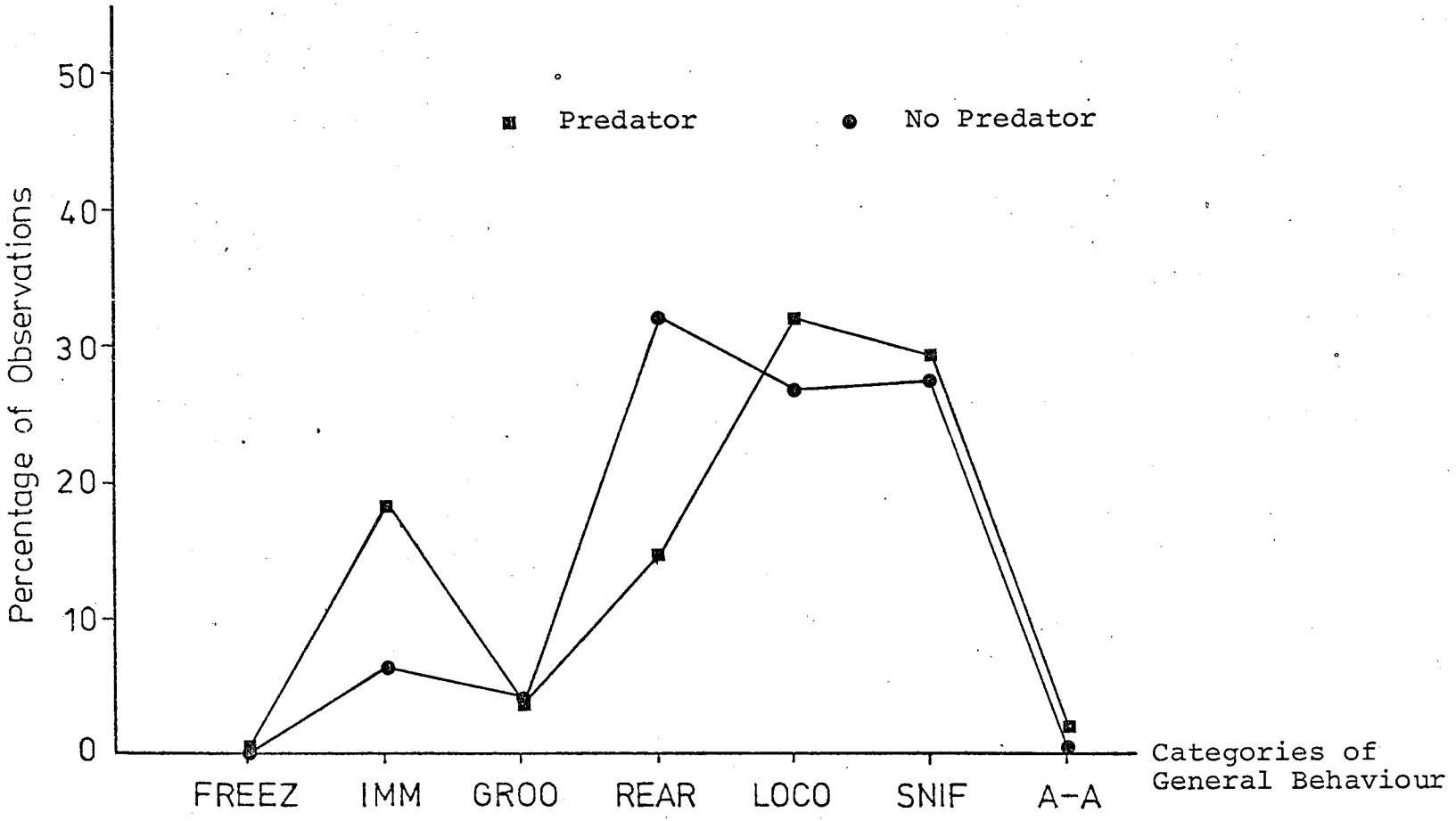

Figure 30 Percentage of Observations of Each Category of Behaviour for the Predator Main Effect

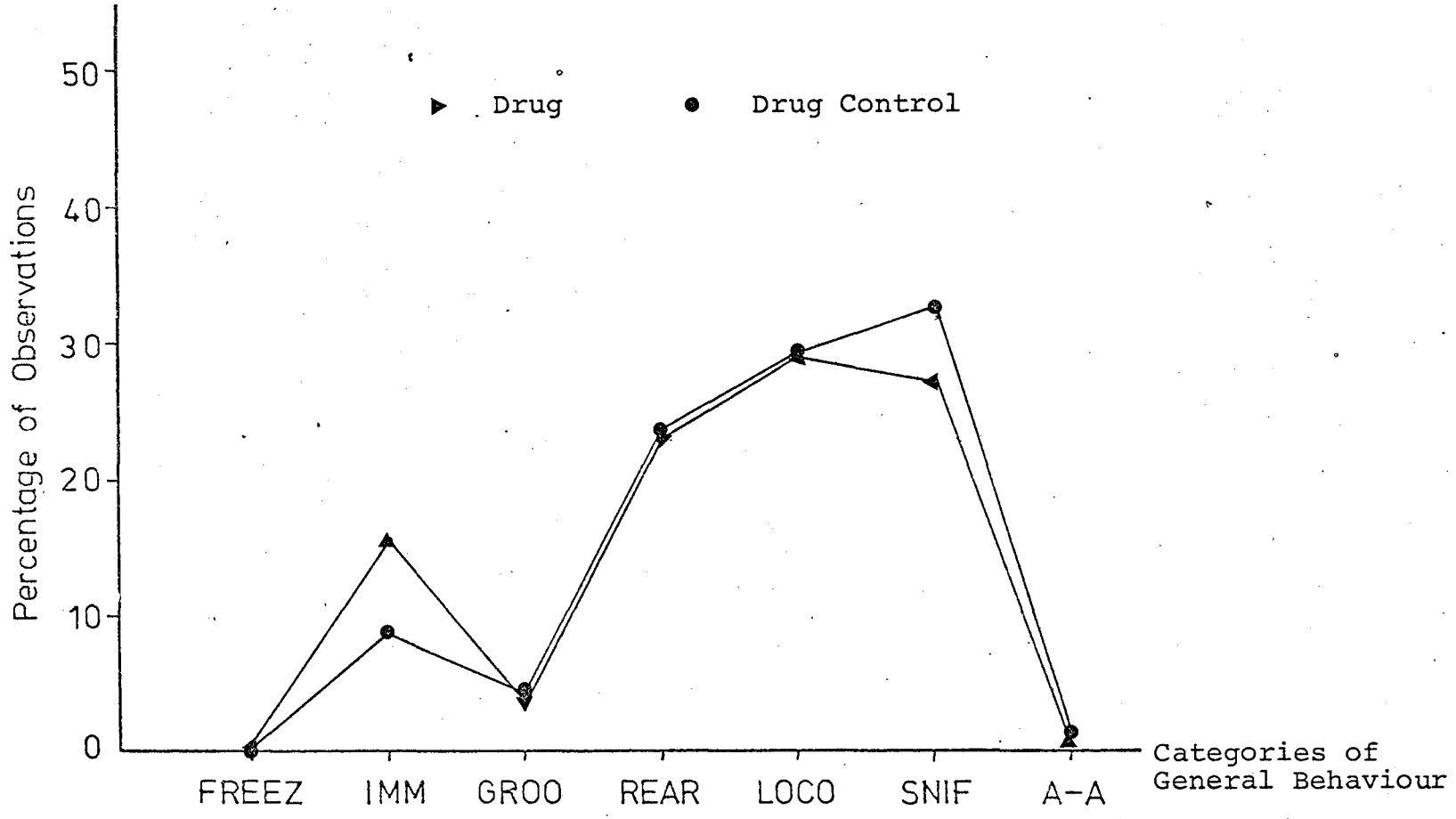

Figure 31 Percentage of Observations of Each Category of Behaviour for the Drug Main Effect.

As this analysis was very lengthy, reporting of the results in a similar style to Analysis One would be both tedious and unenlightening. For the purpose of illustration, one dependent variable (Immobility) was chosen for study.

The correlation between IMM 1[1] and IMM 2 was 0.528, between IMM 1 and IMM 3 it was 0.575, and between IMM 2 and IMM 3 it was 0.664. This suggests a moderate association between all three time periods.

For Factor A (strain), immobility was significant over all three time periods at the $p < .001$ level, the direction of results being that Wistars were significantly more immobile than Hoodeds. This is represented in Figure 32.

As can be seen from Figure 32, the trend of the immobility data for the strain main effect was similar over time, with no attenuation of immobility. There was a slight increase in immobility over time which by inspection does not appear to be significant.

The univariate F test for immobility in Factor B (sex) was not significant on any of the three time periods.

For Factor C (predator), immobility was significant over all three time periods at the following levels: IMM 1 = $p < .037$, IMM 2 = $p < .001$ and IMM 3 = $p < .001$. The direction of results was that animals in the predator condition were significantly more immobile than those in the control condition (Figure 33).

As can be seen from Figure 33, the trend of data for immobility in the predator main effect was similar over all three time periods. There was a slight increase in immobility over time in the predator condition but not in the control.

1. IMM 1 refers to the first third of the observation time, IMM 2 to the second third and IMM 3 to the last third.

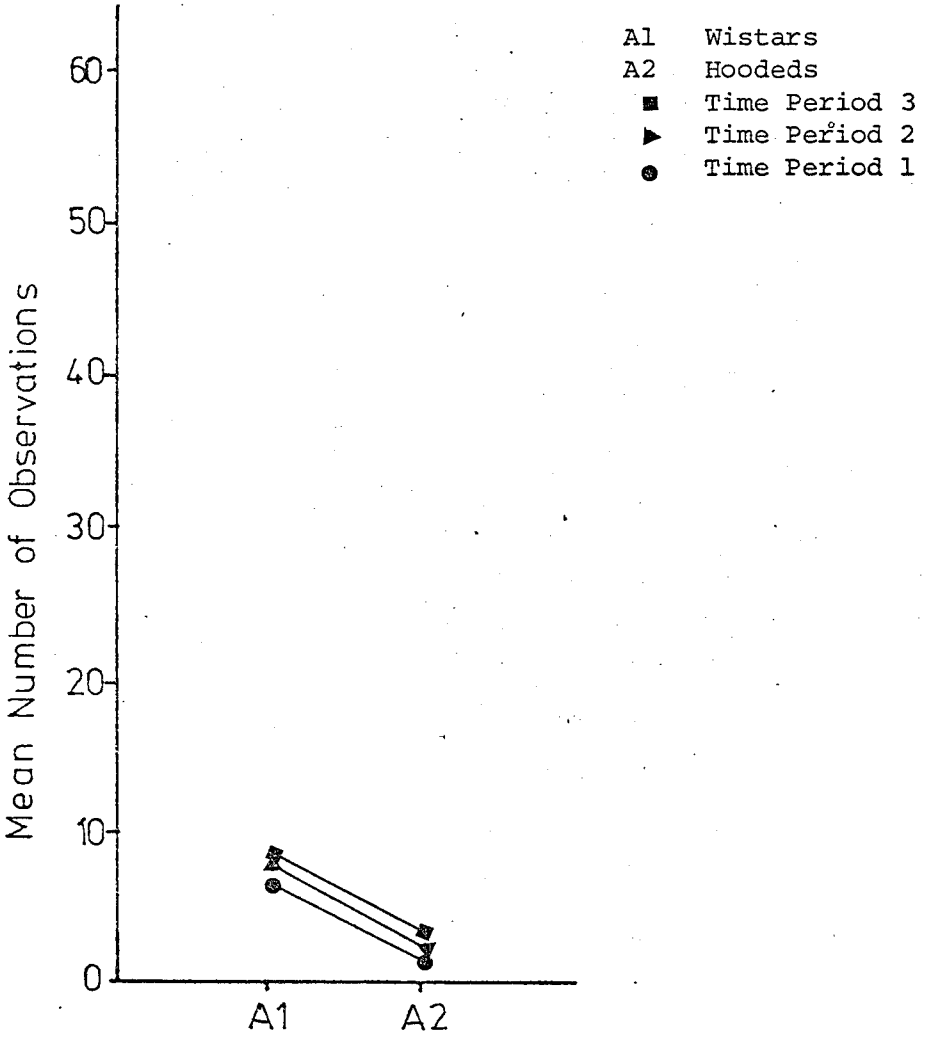

Figure 32 Immobility Scores for the Strain Main Effect Divided into Three Time Periods

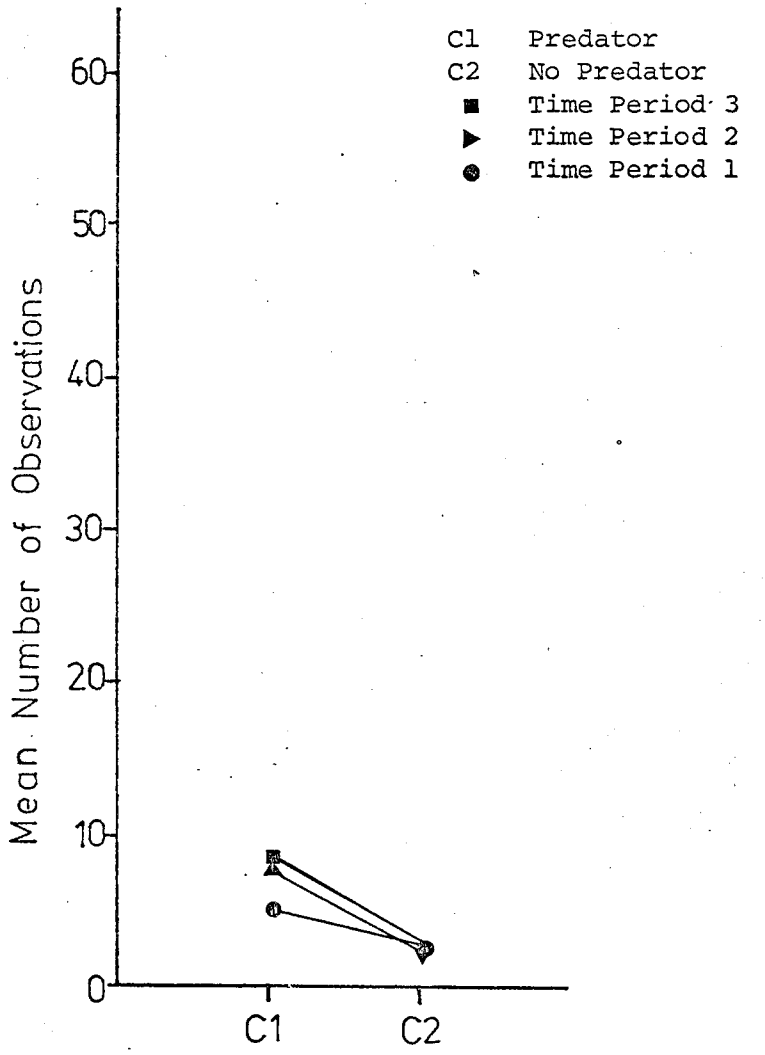

Figure 33 Immobility Scores for the Predator Main Effect Divided into Three Time Periods

The multivariate F test for Factor D (drug) was not significant.

None of the interactions yielded significant multivariate results except for AD (strain x drug) and immobility was not significant there.

Examining one criterion demonstrated that time was not an important variable and in fact a shorter observation period would have yielded similar results to Analysis One. Whilst acknowledging that this brief inspection of time only dealt with one criterion, similar observations could be made about all the other criteria with the exception of locomotion and lines crossed which decreased over time in all conditions. Table 8 (in the appendix) reports the results in full.

In conclusion, time did not appear to be an important variable in this study.

CHAPTER FOUR

DISCUSSION

4.1 INTRODUCTION TO THE DISCUSSION

The major emphasis of this research was the examination of the reactions of two strains of rat to a predator, and the modification of these reactions by chlordiazepoxide. The adequacy of the present methodology in studying these reactions was also thought to be important. Thus, the discussion below will centre around these considerations.

Subsidiary points of interest were the effects of gender and strain on both defensive reactions and the drug modification of these reactions.

In order to discuss the results, the dependent variables will be considered in three categories: measures of freezing, measures of flight and other measures.

4.2 MEASURES OF FREEZING

Two criteria were used to directly measure freezing (immobility and freezing) and a further two criteria were used as indirect measures of freezing (locomotion and lines crossed).[1]

There is considerable variability in the literature in both definitions of freezing and in the manner in which it is measured. All four of the variables under consideration have been used in other research to measure the freezing SSDR. The most stringent definition of freezing was adopted by Curti

1. All dependent variables were defined in Chapter 2.

(1935), who recorded freezing when all activity had ceased for at least three minutes. Other authors, including the present one, recorded freezing if the animal was immobile without vibrisa movement (Bolles and Riley, 1973; Bronstein and Hirsch 1976; Fukunaga, personal communication; Grossen and Kelley, 1972). However, most of the work done by Blanchard and Blanchard assumed that freezing is reflected in low locomotion and low lines crossed. As pointed out in an earlier section, inactivity as measured by locomotion and lines crossed does not necessarily measure freezing. In this study, freezing was associated in a negligible manner with both locomotion and lines crossed ($r = -0.008$ and 0.001 respectively). Thus, direct measurement of freezing did not correspond to the measures of locomotion and lines crossed. Furthermore, Archer (1973) states that low ambulation (locomotion) is an unreliable measure of fear or emotionality. As freezing was a rare occurrence in the present research (no-predator animals froze 0.0% of the time and predator animals froze 0.13%), low correlations were to be expected. Low frequency of freezing was also noticed by Bronstein and Hirsch (1976). Other studies have found high levels of freezing, however. Research has demonstrated that low frequency of freezing is associated with (i) availability of escape (ii) familiarity with the presence of an escape route (Blanchard, Fukunaga and Blanchard, 1976) and (iii) a threat stimulus that is highly discriminable (Blanchard and Blanchard, 1969). The present research design used a highly discriminable stimulus (a predator), allowed escape, and in habituation the animals were able to discover

that escape was possible. The low frequency of freezing in this research thus confirms prior research. High levels of freezing observed in other studies were due to inadequate definitions of freezing, unavailability of escape, and poorly discriminable testing situations (for example, footshock delivered through a grid floor).

Although freezing occurred rarely, there was a significant result concerning freezing in the present study; freezing occurred significantly more often in the predator condition than in the control condition. This confirmed previous findings (Blanchard and Blanchard, 1969a,b; 1970; 1971; Curti, 1935).

Immobility corresponds more closely to other studies' definitions of freezing. It was correlated slightly with freezing (0.325) and negatively with both locomotion and lines crossed to a moderate extent (-0.494 and -0.453 respectively). These associations are not high enough to warrant the assumption that lines crossed and locomotion measure either freezing or immobility. However, immobility does seem to approximate these criteria more closely than freezing, adding some weight to the notion that other studies really measured immobility while calling it freezing.

Immobility was highly significant for a number of main effects and interactions, and contributed in a major way to all the significant multivariate results.

Immobility was found to be significantly greater in animals in the predator condition than those in the no predator condition, which is consistent with the freezing results. This trend was observed in both strains of animals, although

Wistars were significantly more immobile than Hoodeds in both predator conditions. Initial tendency to immobility in Wistars was at an equivalent level to Hoodeds in the predator condition. Greater immobility in Wistars is consistent with other work (Hughes, 1973) and this could be due to either genetic variables or the reduced early handling the Wistars received, as strain was confounded with handling in the present research. The direction of the interaction between strain and predator suggests early experience and genetics may be important modifiers of immobility in relation to threat. Another interaction (strain x sex x predator) also showed this strain difference but males showed less reactivity to the predator than females. In particular, Wistar females demonstrated the greatest level of immobility in the predator condition. Further study of the effect of gender is indicated before unequivocal interpretations are made. In this study, immobility rather than freezing more accurately measured reactions to a predator. Possibly immobility should be seen as a close approximation to freezing and therefore on the SSDR continuum. As the situation was both escapable and easily discriminable, it could be considered surprising that even immobility occurred frequently. However, compared to other behaviours, immobility was never a high frequency behaviour (presence of the predator raised its frequency from 6.55% to 18.02%). Furthermore, the present apparatus allowed for escape and then immobility to occur, due to escape being defined as distance from the predator rather than actual movement. The apparatus did not allow absolute escape as even from the far end of the runway the animals were able to at

least smell, and sometimes see, the ferret. Escape from close proximity to the predator was available but not escape from all the situational cues. Some response competition does appear to have occurred.

Drug administration increased immobility. There was no significant interaction between drug and predator conditions for immobility ($p < .07$) but inspection of the means indicated the increase in immobility when drugged was highest for animals in the predator condition. Other studies found both amygdaloid and hippocampal lesions disrupted freezing (Blanchard and Blanchard, 1972a, 1972b), reduction in freezing occurring once the predator was introduced but not before. Plotnik et al. (1974) found scopolamine administration also reduced freezing in the presence of a predator. Rather than attenuating immobility, Chlordiazepoxide increased it both with and without presence of a predator. While one cannot conclusively say that chlordiazepoxide disrupted immobility reactions to threat due to the non significance of this interaction, the trend of the data certainly indicates this conclusion. At the level of speculation, possible reasons for this could be due to the disruption of hippocampal theta by chlordiazepoxide. If the hippocampus is involved in mediating the freezing SSDR as suggested by prior research, and if chlordiazepoxide renders the hippocampus more reactive to stimuli (Schallek et al., 1964), one might expect increased freezing and immobility. As lesions to the hippocampus decrease freezing (Blanchard and Blanchard, 1972a, 1972b) enhancing the reactivity of the hippocampus should increase sensitivity to reactions to threat. Unfortunately, due to conflict over the role of the hippocampus, either increased or decreased

immobility could be explained to suit either theory. Possibly it is 'safer' to merely state that disruption occurred.

Lines crossed has been assumed in other studies to indirectly measure freezing but was not correlated significantly with it in this study and was correlated only moderately with immobility.

Only one significant result occurred for lines crossed and this was not related to presence of the predator. The sex main effect for lines crossed was significant with females crossing more lines than males. The only study comparing sex differences (Blanchard and Blanchdard, 1970) also found male control subjects were reliably less active than female control subjects but unfortunately they confounded age with sex.

Lines crossed not only did not measure freezing in this research but also was not found to be a good discriminator.

Locomotion is the final measure which has been thought to relate to freezing but it was not correlated significantly with freezing in this study although it did correlate moderately with immobility. Locomotion was a frequent behaviour regardless of condition, occurring approximately 30% of the time.

Animals in the predator condition locomoted significantly more than those in the no predator condition. However, this is not consistent with other results. Blanchard and Blanchard (1971) found animals in the presence of a cat moved less than controls and experiments using shock as a stimulus found similar results (Blanchard and Blanchard, 1969b, 1972b) as did those using scopolamine (Plotnik et al., 1974).

Although immobility and locomotion were not perfectly correlated, one would have expected locomotion to decrease in the presence of a predator because immobility increased. High levels of both immobility and locomotion in the presence of the predator suggests that both were high frequency behaviours so that if immobility was not occurring then locomotion was, and vice versa. Higher locomotion in the predator condition could be due to escape activity, as escape was possible in this apparatus.

Wistars were found to locomote significantly more than Hoodeds. However, when drugged, Wistars decreased locomotion while Hoodeds increased locomotion. Variable results have been found on locomotion after chlordiazepoxide administration, some studies observing an increase, others a decrease, and some no change at all. Christmas and Maxwell (1970) and Hughes (1972) suggested a dose dependent inverted U curve of activity existed. Hughes (1972) found increased locomotion in male Hooded rats on doses of 2.5 and 3.75 mg/kg of chlordiazepoxide and no effect on saline and 5.0 mg/kg. Thus the present dose of 4.0 mg/kg would be expected to increase locomotion, and doses higher than 5.0 mg/kg to reduce it, due to central nervous system depressant effects. Plotnik et al. (1974) also found increased locomotion after administration of scopolamine in Hooded rats. The strain difference in locomotion found in the present study after drug administration may be explained as follows. Hooded rats increased locomotion after drugging which was consistent with the dose administered and other studies' results. The Wistars' decreased locomotion may be due to heightened emotionality in these animals affecting reactivity to the drug so that the effect was more

like that of a higher dosage. The interaction of strain x sex x drug demonstrates that Hoodeds of both sexes increased locomotion when drugged (especially Hooded males). However, Wistar females only marginally increased locomotion and Wistar males markedly decreased locomotion, when drugged. Thus the strain effect of drug administration is mainly due to the reduction in locomotion in Wistar males.

It is worth noting, at this point, that reliance on locomotion as a measure of immobility or freezing would have resulted in the conclusion that immobility was reduced by drug administration while the opposite is true.

4.3 MEASURES OF FLIGHT

There were two measures of flight or escape used in this study. The first of these was latency to leave the startbox and the second was position in the runway which was measured by number of times observed in each of the five portions of the runway.

Latency to leave the startbox, which was in close proximity to the stimulus animal, was expected to decrease in the presence of the predator. It was assumed that as SSDRs are pre-experimentally acquired, they should appear in laboratory animals and should occur rapidly. As the animals had the opportunity to discover, during habituation, that escape from the startbox was possible, escape would be expected to be both rapid and prepotent over freezing. However, latency was never significant although it approached significance in the predator main effect ($p < .062$). The direction of this was for animals in the no predator condition to take longer to

leave the startbox than those in the predator condition and this was consistent with expectations. Failure of latency to discriminate between conditions more clearly could be a function of the way in which it was measured. It was recorded in multiples of four seconds and possibly if a finer, more precise method of measurement had been used, results would have been more striking.

Position in the runway was measured by noting which of the five segments the rat was in. Obviously, long periods of time spent in one portion of the runway automatically decreased time spent in the remaining parts. Regardless of sex or strain, animals in the no predator control condition spent most of their time in Cell 1 (53.25%), a moderate amount in Cell 2 (20.71%) and very little in Cells 3, 4 and 5 (7.92%, 8.77% and 9.32% respectively). Introduction of the predator changed this radically so that most of the time was spent in Cell 2 (43.42%), very little in Cells 1, 3 and 4 (17.13%, 10.95% and 10.46% respectively), and a moderate amount in Cell 5 (18.05%). Escape in the predicted form (of retreat as far away as possible) did not occur, but escape from the immediate vicinity of the predator did occur. Preferance for Cell 2 in the predator animals may be explained because this part of the runway was the only one allowing some measure of 'safety' or distance from the predator while at the same time allowing visual and olfactory exploration of the predator. Also, Cell 2 was positively correlated with immobility (0.369) suggesting presence in Cell 2 and immobility often occurred together. Availability of extra area to escape into, did not prove to be important in the present research. Kim et al. (1971) used

a fear index in which they compared first channel (closest to the predator) and fourth channel beam interruptions. Unfortunately they did not include data for the middle sections so they cannot be compared with present results. However, their results also indicated that the animals shunned close proximity to the predator. This was the only study using apparatus comparable to this one. Preference for Cell 1 in no-predator animals in the present research may be due to this segment of the runway being a more 'interesting' part of the runway. It was made of different materials to the rest of the runway and allowed more sensory stimulation, particularly from the stimulus rat in the arena.

Although flight was not reflected in large amounts of time in the far end of the runway, animals in the predator condition were significantly more often in Cell 5 than those in the no predator condition. However, results concerning Cell 5 should be interpreted with caution as they did not contribute to the multivariate significance in any of the tests.

Other studies found avoidance of an approaching cat occurred, but not avoidance of an approaching hand (Blanchard and Blanchard, 1971). They also found that the same stimulus cat that elicited avoidance when escape was possible, elicited freezing when escape was punished. One can conclude that the present results support other findings concerning escape in the presence of a predator although the hypothesis that escape to the far end of the runway would occur, was not supported.

Drug administration resulted in significantly increased time in Cell 1 (increased from 31.88% in the drug control condition to 38.54% when drugged) and significantly decreased

time in Cell 5 (16.9% to 10.42%), regardless of predator condition. However, animals in the predator condition showed a more marked decrease in presence in Cell 5 when drugged. The increase in Cell 1 when drugged occurred in both sexes and strains except that Wistar females decreased presence in Cell 1 when drugged. This sex x strain x drug difference was also evident in Cell 5, where Wistar females increased time in Cell 5 when drugged while the other subjects decreased time in Cell 5. The decrease in presence in Cell 5 in drugged animals in the predator condition cannot be explained by a general decrease in presence in Cell 5 as it was more marked in these animals, indicating some attenuation of escape behaviour occurred after chlordiazepoxide administration. However, there were no other significant predator x drug interactions except that drugging increased presence in Cell 2 regardless of sex in the no predator condition, while predator males also increased time in Cell 2. The reverse was true for females in the predator condition. As presence in Cell 2 increased in the no predator condition as well as for males in the predator condition after drugging, no importance can be attached to this increase with regard to escape behaviour. Chlordiazepoxide has been found to interfere with the conditioned escape response although conflicting results have been demonstrated in classical avoidance trials (Cicala and Hartley, 1965). Thus the present results to some extent support the conditioned escape literature.

One can conclude that chlordiazepoxide administration affected presence in Cells 1 and 5, regardless of presence or absence of predator and there was some strain and sex

modification of this. There was no firm evidence for disruption of flight reactions to a predator by the drug, particularly as disruption occurred also in no predator animals. However, there was some attenuation of escape behaviour in drugged animals in presence in Cell 5 which accentuated trends observed in the no predator animals. As escape was reflected by presence in Cell 2 regardless of drug condition, drug modification of this variable in the presence of the predator would have been illuminating. However, there were sex differences in this variable, attenuation of escape to Cell 2 occurring in females and facilitation occurring in males when drugged. Further research to clarify the role of gender and chlordiazepoxide modification of escape behaviour is indicated.

4.4 OTHER MEASURES

Grooming is a variable which is often ignored in psychological research. This variable has often been viewed as an index of fearfulness or emotionality and has been observed in conflict situations. Others view it simply as a measure of general activity. Grooming, in the present study, was a behaviour that seldom occurred and resulted in only one significant test on the strain x sex x predator interaction. This complex interaction is difficult to interpret and the most that can be said about it is that animals with an initially low level of grooming increased grooming in the predator condition while animals with higher initial levels reduced grooming in the predator condition. Any meaningful conclusion from these results is impossible and grooming was the least informative measure used.

Rearing is sometimes regarded as a measure of general activity because there is disagreement over whether rearing indicates exploratory tendencies, emotionality or C.N.S. excitability (Archer, 1973). Rearing was a common behaviour observed in the present research, occurring approximately 24% of the time. It did not correlate highly with locomotion (0.240) but did with immobility (-0.646) suggesting comparison between rearing and immobility results would be more meaningful than with the locomotion results.

Animals in the predator condition reared significantly less than those in the no predator condition which is consistent with both immobility findings and other research with predators and juveniles (Bronstein and Hirsch, 1976). This decreased rearing in the predator condition was evident in both strains and sexes but Wistars reared less than Hoodeds. The latter finding is consistent with Hughes (1973) findings and with the higher immobility observed in Wistars.

The strain x sex x drug interaction showed drugged Hooded females and Wistar males increased rearing while the opposite occurred in Wistar females and Hooded males. This grouping of sexes and strains when drugged also occurred in other variables (locomotion and cell 1) and may be an interaction of sex differences and emotionality. Variability in response suggests other extraneous variables are important. Rearing has been found to decrease with increasing dose strength of chlordiazepoxide (Hughes, 1972) and this is consistent with immobility results and some of the rearing results in this study.

Sniffing is another variable that is virtually never considered in the literature. Although sniffing was a low frequency behaviour in all conditions, it was found that Hooded rats sniffed more than Wistars and undrugged animals sniffed more than drugged ones. The latter result may be due to interference in olfactory perception by the drug. However, impaired olfactory perception does not explain other results in this study. For example, immobility increased in the presence of the predator in drugged animals (although not significantly so) demonstrating if anything increased sensitivity to the predator.

The strain x predator interaction showed that Hoodeds increased sniffing in the presence of the predator while the reverse was true of Wistars. As Hoodeds sniffed more than Wistars, even in control conditions, their greater use of olfactory cues may be reflected in increased sniffing in a threatening situation. The decrease in sniffing demonstrated by Wistars could be due to the greater immobility demonstrated by these animals in a threatening situation.[1]

The final variable for consideration is the approach-avoidance variable. This variable was a low frequency behaviour which was virtually never seen except in the predator condition. It occurred almost exclusively in Cell 2, with the animal 'hovering' at the entrance to Cell 1. Hooded rats were found to indulge in this behaviour more frequently than Wistars. While speculation about the motivation of animals could be viewed as anthropomorphic, the animals appeared to be

1. Because the measurement of categories of general behaviour was ipsative, any high frequency behaviour must lower the frequency of other behaviours and vice versa. Some significant results may thus be statistical artifacts.

both curious and fearful of the predator. Animals, regardless of strain, significantly increased approach-avoidance in the predator condition. Drugging decreased approach-avoidance. However, the predator x drug interaction showed that drugging increased approach-avoidance in no-predator animals and decreased it in predator animals. This suggests that introduction of the predator increased fear so that SSDRs such as immobility took over and weaker responses such as approach-avoidance decreased. The initial approach-avoidance in the no predator condition could be due to the aversiveness of the drug state. Possibly, approach-avoidance occurs in moderately fear evoking situations such as a mildly aversive drug state, and disappears in both highly fear evoking and no fear situations. The decrease in approach-avoidance when drugged in the presence of a predator does not suggest that fear was attenuated by the drug since immobility (a measure of fear) increased. It merely suggests a stronger behaviour (an SSDR) becomes prepotent. The reasons for Hoodeds showing higher levels of approach-avoidance than Wistars is consistent with this notion of approach-avoidance appearing in moderately fear evoking situations, as the Hoodeds showed lower levels of fear on other measures. Alternatively, approach-avoidance may be regarded as adaptive if it occurred after an SSDR occurred, intermediate to other behaviours becoming more probable, as it allows greater exploration of the environment than either freezing or immobility. Clearly such discussion is speculative but it does suggest an important area for investigation. Other studies have not reported the phenomenon of approach-avoidance which could indicate it was a product of the present apparatus or that they recorded it as some other category of behaviour such as locomotion.

4.5 GUIDELINES FOR FURTHER RESEARCH

As in most research, weaknesses in the present design become increasingly apparent to the author, suggesting important modifications for future research.

Due to the limitation of time available, one strain of rats (Wistars) could not be born and raised in the same laboratory as the other strain, and consequently did not receive as much early handling as the Hoodeds. Thus the genetic difference of strain was confounded with handling, limiting interpretation about strain differences. Other relevant studies either used unhandled rats or failed to report the handling history of their subjects. Earlier reports of clear results with wild animals but variable results with laboratory animals in response to a predator (Curti, 1935) suggest 'tameness' in animals may attenuate responses. The present finding of strain differences in reactivity to the predator and the drug may be a function of handling or strain affecting emotionality or reactivity of the animals.

Housing conditions may also have been important in the present results. The majority of relevant studies used individual as opposed to group housing. As individual housing is known to be aversive, causing emotional disturbances on a number of behavioural correlates (Hahn, 1965; Moyer and Korn, 1965), it was considered more relevant to house the animals in the present study in groups. Studies relevant to the present research have maximised initial emotionality in their subjects by housing them individually and not handling them. Possibly the constellation of fear responses described by the authors

of these studies are due to a certain extent to high levels of initial emotionality. The same constellation of responses were apparent in 'tamer' animals in this study but not to the same degree as animals with a higher initial level of emotionality. This notion could be investigated in future research by a number of ways: manipulation of handling, housing and artificially induced emotionality.

Another fault in the present design was that the experimenter was present in the testing room. This had the added problem of not enabling reliability checks to be carried out, since addition of an extra individual at random intervals could have further influenced results. Videotaping, one way screens, or mirrors could have circumvented this problem. Electronic recording of data by methods such as photocells is not always reliable and would not have yielded as much information as the present study.

A problem for all studies in this area is the difficulty in selecting an adequate control for the predator. In general, other relevant studies left the stimulus area empty for the control condition. However, movement has been found to be the most important component of the predator stimulus (Blanchard, Mast and Blanchard, 1975; Curti, 1935). Control of a novel stimulus was also seen to be important. These considerations resulted in a small non-predator animal being chosen as a more appropriate control than empty space. The results could not then be attributed to presence of a moving object rather than the predator stimulus. The use of a number of controls may isolate the most appropriate control for a predator.

Further investigation of drug modification of SSDRs could involve a range of drugs with a number of different doses.

4.6 CONCLUSIONS

This research has demonstrated the need for naturalistic investigations of species-specific defense reactions. Although many earlier observations have been confirmed, a more precise method of defining dependent variables has yielded a wealth of information.

Drug modification of reactions to threat has proved a worthwhile addition to the present literature, but much further research is indicated. Conclusions about the central brain structures' role in controlling the appearance and maintenance of SSDRs, are premature at this stage.

The most salient findings of the present study were the alteration in level of many of the dependent variables by introduction of a predator, and drug modification of many of these measures. The notion of freezing and escape constituting SSDRs was upheld, with some modification and extension of the definitions of these variables.

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APPENDIX 1

Table 7. Within Cells Correlations of Criteria With Standard Deviations on Diagonal[1]

Variable	FREEZ1	FREEZ2	FREEZ3	IMM1	IMM2	IMM3	GROO1	GROO2	GROO3	REAR1	REAR2	REAR3	LOCO1	LOCO2	LOCO3	SNIF1	SNIF2	SNIF3
FREEZ1																		
2																		
3																		
IMM1																		
2				0.528														
3				0.575	0.664													
GROO1																		
2							0.408											
3																		
REAR1				-0.533	-0.413	-0.455												
2					-0.393	-0.348												
3				-0.422	-0.365	-0.537				0.375	0.358							
LOCO1				-0.395	-0.404													
2					-0.440								0.323					
3						-0.395								0.334				
SNIF1				-0.302						-0.353								
2											-0.445						0.351	
3												-0.355						
A-A 1																		
2																		
3									0.326									
CELL1 1																		
2																	0.319	
3																		
CELL2 1			-0.324	0.346						-0.382				-0.320				
2					0.406									-0.309				
3					0.352							-0.331						
CELL3 1														0.324				
2																		
3			0.323															
CELL4 1			0.496															
2																		
3																		
CELL5 1																		
2								0.359										
3												0.329						
LXX1				-0.449	-0.334	-0.359				0.324	0.380		0.406					
2				-0.330	-0.381	-0.258				0.301	0.343			0.312				
3				-0.378	-0.405	-0.550					0.341		0.388					
LAT																		

1. Only correlations above ±.300 are recorded.

Table 7 (continued)

Variable		$A\text{-}A_1$	$A\text{-}A_2$	$A\text{-}A_3$	$CELL1_1$	$CELL1_2$	$CELL1_3$	$CELL2_1$	$CELL2_2$	$CELL2_3$	$CELL3_1$	$CELL3_2$	$CELL3_3$	$CELL4_1$	$CELL4_2$	$CELL4_3$	$CELL5_1$	$CELL5_2$	$CELL5_3$	LXX_1	LXX_2
A-A	1																				
	2																				
	3																				
CELL1	1																				
	2				0.360																
	3				0.314	0.519															
CELL2	1	0.311			-0.499																
	2					-0.586		0.436													
	3					-0.366	-0.569		0.613												
CELL3	1																				
	2					-0.454															
	3								-0.319												
CELL4	1				-0.444			-0.356			0.426										
	2					-0.336															
	3									-0.352		0.309			0.480						
CELL5	1				-0.435	-0.319	-0.314	-0.400					0.306	0.451	0.320						
	2							-0.447	-0.400								0.531				
	3						-0.324			-0.383							0.347	0.470			
LXX	1				-0.304						0.534			0.557							
	2		0.402			-0.440						0.520			0.480	0.338				0.494	
	3												0.379			0.418				0.521	0.505
LAT					0.340																

APPENDIX 2

Table 8. Means of the Main Effects[1]

Variable	FREEZ			IMM			GROO			REAR			SNIF			LOCO			A-A		
FACTOR	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
A 1	0.0	0.05	0.10	6.44	7.66	8.31	1.03	1.81	1.75	8.15	8.18	7.92	9.8	9.8	9.93	14.5	12.35	11.8	0.18	0.37	0.26
2	0.03	0.00	0.00	1.32	2.28	3.30	1.17	2.01	1.65	10.67	11.28	10.74	14.0	13.9	14.05	12.6	9.90	10.2	0.53	0.59	0.65
p<				.01	.01	.01				.013	.003	.004	.001	.001	.001	.006	.002	.004	.026		
B 1	0.03	0.00	0.08	4.28	5.39	6.03	0.90	1.56	1.56	10.23	9.93	11.14	11.50	12.00	11.64	12.90	10.80	10.40	0.41	0.53	0.37
2	0.00	0.05	0.03	3.49	4.55	5.57	1.30	2.26	1.84	8.59	9.53	8.76	12.30	11.70	12.34	14.20	11.40	11.50	0.30	0.42	0.55
p<																.043					
C 1	0.03	0.05	0.10	5.05	7.60	8.72	0.97	2.08	1.58	6.09	6.10	5.90	12.10	12.10	11.64	15.20	11.80	11.70	0.68	0.95	0.91
2	0.00	0.00	0.00	2.72	2.34	2.88	1.24	1.74	1.82	12.74	13.50	12.80	11.70	12.30	12.84	11.90	10.40	10.30	0.03	0.00	0.00
p<				.037	.001	.001				.001	.001	.001				.001	.053	.045	.001	.001	.001
D 1	0.00	0.00	0.03	3.17	3.53	3.99	1.26	2.15	1.63	9.60	9.70	10.00	12.30	12.50	13.49	13.50	11.50	10.80	0.44	0.63	0.76
2	0.03	0.05	0.08	4.59	6.41	7.62	0.95	1.66	1.77	9.40	9.90	8.80	11.50	11.10	10.50	13.60	10.70	11.20	0.26	0.33	0.16
p<					.01	.003									.002						.023

Variable	CELL 1			CELL 2			CELL 3			CELL 4			CELL 5			LXX			LAT
FACTOR	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	
A 1	15.46	14.74	12.87	12.74	12.66	14.0	3.66	3.60	3.49	2.98	3.15	3.84	5.21	5.77	5.92	23.21	19.02	18.27	15.01
2	13.78	14.22	13.33	13.22	11.59	12.59	4.30	3.67	4.13	3.63	4.97	4.57	5.07	5.49	5.38	23.61	16.57	14.49	21.26
p<											.003							.032	
B 1	15.25	14.39	13.62	12.67	12.02	13.25	4.16	3.87	3.82	3.17	4.38	3.92	4.79	5.30	5.61	25.67	18.60	17.23	18.84
2	13.99	14.57	12.63	13.28	12.34	13.34	3.80	3.40	3.80	3.45	3.74	4.48	5.49	5.97	5.67	21.15	16.99	15.53	17.42
p<																.035			
C 1	6.77	7.14	6.70	18.01	16.37	17.54	5.16	3.91	4.22	3.67	4.61	4.21	6.44	7.88	7.32	26.72	17.40	15.27	8.26
2	22.47	21.82	19.55	7.95	7.88	9.05	2.80	3.36	3.40	2.94	3.51	4.19	3.84	3.38	3.99	20.11	18.44	17.49	28.01
p<	.001	.001	.001	.001	.001	.001	.001				.057		.005	.001	.001	.002			.062
D 1	13.22	12.78	12.22	12.73	12.24	12.61	3.95	3.55	3.86	3.49	4.65	4.28	6.61	6.65	7.05	23.17	18.24	16.72	11.67
2	16.02	16.18	14.04	13.17	12.02	13.98	4.01	3.72	3.76	3.12	3.46	4.13	3.67	4.61	4.25	23.65	17.35	16.04	24.59
p<	.043	.044									.046		.002	.027	.003				

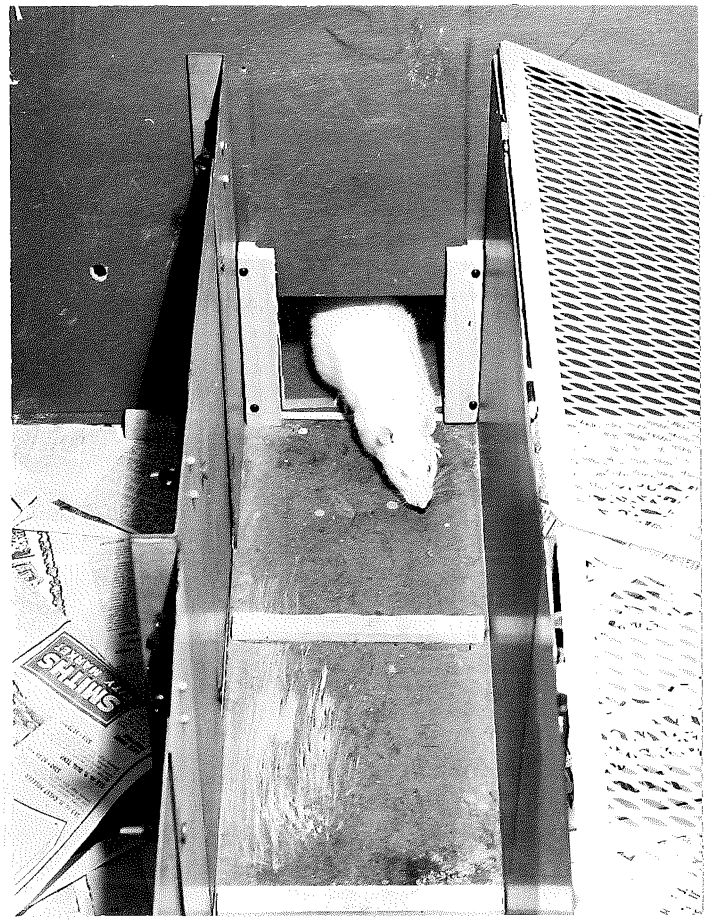
1. Interactions were not significant.

Appendix 3 A

The Apparatus

Appendix 3 B

Rat Entering Cell 2 of the Runway from the Perspex Enclosure



Appendix 3 C

Rat in the Perspex Enclosure with Stimulus Animal (no Predator Control) in the Arena

Appendix 3 D

Rat Leaving the Perspex Enclosure with Predator (Ferret) in the Arena